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INTERPRETIVE MORPHOLOGY AND TAXONOMY OF BRYOZOAN GENUS TABULIPORA

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ABSTRACT

Tabulipora YOUNG, 1883, is an upper Paleozoic bryozoan genus having *T. urii* (FLEMING, 1828) as its type species by monotypy. A lectotype for *T. urii* is selected herein from the syntypes which were collected and partially figured by URE in 1793.

All species of *Tabulipora* possess perforate transverse partitions which are called ring septa in this paper. The growth of these structures near the apertures of the zooecia by concentric addition of laminae, and the common kidney-shaped form of the distally offset perforations (foramina) suggest that they were the anterior walls of the living chambers. Diaphragms (transverse partitions without perforations), which probably formed the posterior walls of the living chambers, are common in Pennsylvanian and Permian species of *Tabulipora*.

In many *Tabulipora* species, zoarial growth increments composed of alternately thin and thick zooecial walls were formed as a result of cyclic fluctuations in the total area of $CaCO_3$ deposition. These growth increments give the walls their characteristic moniliform appearance in longitudinal sections. Branch extension accelerated during the thin-walled phases of the growth cycles, as indicated by increase in length of the thin-walled segments nearer the branch axis. During the thick-walled phases, however, branch extension must have been slower because the thick-walled segments do not vary significantly in length between the exozone and the central portions of the endozone.

Possible fossilized brown bodies in *Tabulipora* zoaria may be an indication that processes of degeneration and regeneration of soft parts took place in these Bryozoa. The restriction of ring septa to thick-walled phases of the zoarial growth cycles in the endozone might then indicate that these portions of zoarial growth cycles were the phases of regeneration, and that no functional polypides were present in the zooecia at the branch tip during the thin-walled phases.

Evolutionary trends from Mississippian species to Pennsylvanian-Permian species include increases in average wall thickness, development of calcified diaphragms, and the development of more regular and well-formed annular thickenings.

INTRODUCTION

Tabulipora YOUNG, 1883, of Carboniferous and Permian age, belongs to the order Trepostomata and is placed by most authors in the family Stenoporidae. Uncertainty about its taxonomic status and morphological characteristics has arisen because of: 1) the manner in which the genus was named; 2) confusion as to what specimens constituted the type series; 3) inability of authors

to locate the type specimens; and 4) mistakes in revisions of the genus. The present revision of *Tabulipora* was undertaken to clarify and correct these problems through a study of the more salient morphological features of the genus, and a re-evaluation of its taxonomic history.

Opinions once held by some workers about the taxonomic status of *Tabulipora* were summarized by CROCKFORD (1957), who stated that its recognition as a valid genus was doubtful, as well as validity of considering *T. scotica* LEE, 1912, as the type species, and that the problems called for application to the International Commission on Zoological Nomenclature. This course of action, however, does not seem necessary. The conclusions presented here are that *Tabulipora* is a valid genus having *T. urii* (FLEMING, 1828) as its type species by monotypy, the syntypes of which originally were described and partially figured by URE (1793, pl. 20, fig. 1-2). A lectotype is selected herein from URE's collection.

Morphologic characteristics of *Tabulipora* were studied using thin sections and acetate peels. Some sections and peels were already on deposit in the University of Kansas Museum of Invertebrate Paleontology and the United States National Museum before this project was initiated. Other sections and peels were prepared from material also on deposit in these two museums and a small amount collected during the course of the work. The peel method used is that of BOARDMAN & UTGAARD (1964).

So that much of the range of variation in *Tabulipora* would be observed, specimens of many species from widely dispersed localities in the United States and a small number of specimens from Nova Scotia, Australia, and Scotland were studied. For some specimens, illustrated on Plates 1-7, incomplete locality and stratigraphic data are given because no further information is available on the older collections from which the specimens came. The work was done during parts of 1966 and 1967 at the University of Kansas and at the Smithsonian Institution, Washington, D.C., under the University of Kansas-Smithsonian Institution cooperative program in paleontology.

PREVIOUS STUDIES

URE (1793, pl. 20, fig. 1-2) figured a fossil (Fig. 1) which he called *Millepore*. His description is (p. 328-329):

> The *Millepore* is a very beautiful genus of the coralloides. It abounds in most of the lime quarries, not only in Kilbride, but in the west of Scotland. The specimens are in fragments, and commonly branched. They are from the thickness of a fine hair, to that of a large quill. Some specimens continue to adhere to the shells, &c. on which they were originally formed, as Fig. 1. The pores are round, and of different diameters in the same specimen, Fig. 2 which is greatly magnified. The extremities of the branches were originally round, as at a. The millepore is frequently spread on the surface of shells, entrochi, &c. like the *Seratula pumila.*

URE apparently did not intend to designate *"Millepore"* as a new generic name; instead, it seems evident that he was referring to *Millepora* LINNÉ.

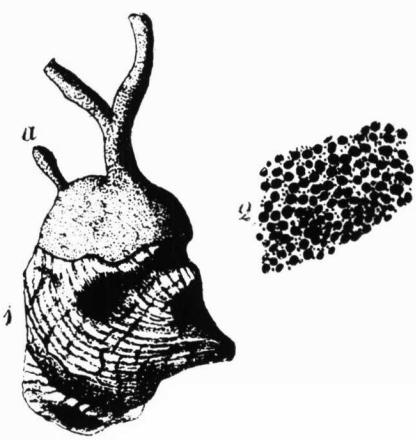


FIG. 1. URE's (1793) figure (actual size) of his "Millepore" specimen: a paralectotype of *Tabulipora urii.*

In the rest of his chapter on "Extraneous Fossils" he used binomial and nonbinomial names of other authors for plants and animals, erecting only three new names for three "families" or "divisions" of pelecypods after stating clearly his intention to do so.

FLEMING (1828) cited URE's figure as an indication for his new species *Cellepora urii* as follows (p. 533):

> *C. Urii.*—Branched, round, about a quarter of an inch in diameter, form round.—Millepore, *Ure* Ruth. 228, t. XX. f. 1.

Thus URE's figured and unfigured specimens became the syntypes of *Cellepora urii.*

YOUNG (1883) proposed the subgeneric name *Tabulipora* in the following statement (p. 158):

> I propose to place provisionally, Ure's "Millepore" in the *Monticulipora* group, under the new subgeneric name of *Tabulipora,* this name being descriptive of its beautiful and interesting internal structure, which, so far as at present known, distinguishes this organism from all its near allies; and at the same time I shall restore to it Fleming's name of *Urii,* after its original discoverer and describer, the Rev. David Ure, the earliest pioneer of Scottish palaeontology.

YOUNG included no other species in *Tabulipora*; thus *Cellepora urii* FLEMING, 1828, is the type species by monotypy.

YOUNG (1883) used *Tabulipora urii* as a name for specimens having perforate diaphragms, here termed ring septa (see section on morphology) in order to distinguish them from *Chaetetes tumidus* PHILLIPS (1836), which ETHERIDGE (1874) stated might be the same as URE's figured specimen. Neither URE nor FLEMING recognized ring septa in *T. urii.* KING (1850) may have been the first to record the occurrence of these structures in specimens now assignable to *Tabulipora* when he discussed an undescribed species of the genus *Calamopora* GOLDFUSS, 1827. He noted (p. 27) that:

> Its tubes are furnished with numerous transverse plates: their walls are foraminiferous; and they are marginated with tubercles; but the transverse plates do not extend to the centre of the tubes; generally little more than half way; the centre is consequently open, at least in the upper part of the tubes, but lower down it becomes closed.

MCCOY (1851, 1855) assigned bryozoans from Britain with ring septa to *Stenopora* LONSDALE (1844), now known to lack diaphragms and septa; but NICHOLSON & ETHERIDGE (1879) challenged this assignment in stating that there was no evidence that MCCOY's specimens belonged to the genus. Rather, they believed that "any appearance of 'perforated diaphragms' in *Stenopora* can only be due to the periodic contractions of the visceral chamber by the annular thickenings of the walls of the corallites, the true tabulae being thin, horizontal, and complete, ..."

After the naming of *Tabulipora,* NICHOLSON & ETHERIDGE (1886) described what they thought were ring septa in *Stenopora howsii* NICHOLSON (1881) and also suggested their presence in *S. australis* NICHOLSON & ETHERIDGE (1886). Nevertheless, at that time they refused to recognize *Tabulipora,* stating (p. 177) with regard to *S. howsii*:

> If no other species of *Stenopora* possessed perforated tabulae, there would be ground for accepting *Tabulipora* as a subgenus of *Stenopora,* or perhaps as a distinct genus. If, on the other hand, the structures above described as occurring in *S. australis* are really perforated tabulae, there does not seem to be any need for a special generic name.

ETHERIDGE (1891, p. 47) concluded, however, that the ring septa of *Stenopora howsii* were of "inorganic origin . . . produced by a postmortem deposition within the cavities of the tubes, as indicated by its presence in some examples and not in others." In the same paper he accepted *Tabulipora* as a distinct and separate genus. (NICHOLSON's slides of *S. howsii* in the Royal Scottish Museum show ring septa.)

ULRICH (1890) described 13 species and three varieties of *Stenopora* from Illinois, all of which possess ring septa; and he included in his generic diagnosis of *Stenopora* the presence of ring septa, probably on account of NICHOLSON & ETHERIDGE's earlier works, which he cites. ELIAS (1957) assigned these species and all other ring-septum-bearing species of *Stenopora* to *Tabulipora,* because *Stenopora* was then known to lack diaphragms and septa. ULRICH (1890) also recorded the discovery of ring septa with foraminal plates in some of his species. His theory about the functions of diaphragms and septa, regarded as correct in this paper, was that the ring septa formed the anterior walls of living chambers, foramina having served as the openings through which moveable soft parts extruded. Ring septa with foraminal plates, essentially diaphragms, were interpreted to be the posterior walls of living chambers.

LEE (1912) revised *Tabulipora* and described new species under that name. He suggested that absorption was used by Bryozoa to remove thickened walls across the distal ends of the branches prior to branch extension and showed how ring septa could appear imperforate if the planes of sections bypassed the foramina. Although he made these positive contributions to the study of Bryozoa, LEE added to the taxonomic confusion about *Tabulipora* by designating *T. scotica* LEE (1912) as type species of the genus in this statement (p. 150):

Genotype: *Tabulipora scotica* sp. nov. [=*Tabulipora urei* Young (pars)]. Carboniferous.

As explained later, the specific name *urei* is not retained here for two reasons. The first is that Young did not really propose it as a new specific name, but assumed his materials to be conspecific with Fleming's *Cellepora urei* and as Fleming's type, i.e. Ure's "Millepore," is lost, the retention of the name would imply specific identity, and this cannot be proved. The other reason is that Young's materials include several species, and as he gave no figures it is impossible to select one as the type with the specific name proposed by Young. But, fortunately, all these species are undoubtedly congeneric, so that the identity of the genus is fully established.

YOUNG did not propose a new specific name but included *Cellepora urii* FLEMING, 1828 in *Tabulipora* as the only species. Since *T. urii* is the type species by monotypy, LEE's choice of *T. scotica* LEE, 1912 has no validity. This invalid designation has been perpetuated in most papers dealing with the genus since LEE's revision.

LEE's spelling of the name *"urii"* as *"urei"* was either a misspelling or an intentional alteration, possibly stemming from earlier misspellings by YOUNG (1888, 1893). Since FLEMING (1828) did not explain the derivation of the name, *"urii"* must stand as the correct spelling according to Article 30, section a, i, 1 of the *International Code of Zoological Nomenclature.*

LEE's work was the last major attempt to revise *Tabulipora.* Aside from a few papers in which species were named, only three major publications concerning the genus have appeared. CUFFEY (1967) described the distribution, morphologic characteristics, and variation in *T. carbonaria* (WORTHEN, 1875), from the Wreford Cyclothem in Kansas. MCKINNEY (1969) described possible organic structures in *T. cestriensis* (ULRICH, 1890). MALECKI (1968), in describing *T. siedleckii* from the Permian deposits of the Sörkapp Land area, Vestspitsbergen, gave a generalized account of colony growth and functional morphology which compares favorably with the more specific interpretations presented here. He also provides an analysis of some of the taxonomic problems connected with the stenoporid genera *Tabulipora, Stenopora,* and *Rhombotrypella.*

Tabulipora presently comprises more than 100 nominal species, some of which may be synonymous. Two genera, *Amphiporella* GIRTY, 1910, and *Sinotabulipora* YANG, 1950, are considered to be junior synonyms of *Tabulipora* for reasons discussed in remarks following the generic definition.

After his death, URE's collection passed into the hands of a Mr. STARK (GRAY, 1865) who later presented it to the Royal Society of Edinburgh. According to W. D. I. ROLFE (personal communication, 1967), in 1909 the collection was deposited in the Hunterian Museum, Glasgow, Scotland, where it now rests; some of the specimens were lost prior to 1909. The collection was borrowed for this revision. None of the specimens resemble URE's figured specimen, a syntype to *T. urii,* so it is assumed that it is one of the missing ones. A specimen chosen from the remainder of URE's collection is designated herein as lectotype of *T. urii.*

MORPHOLOGY

MORPHOLOGICAL TERMINOLOGY

Some terms in this paper are new; others are old terms not used recently in studies of *Tabulipora.* Most are defined where they first appear in the text. In the systematic descriptions, **mural lacunae** is a term used by BOARDMAN (1960), and **mural tubulae** is a new one coined by him but not yet published. They refer respectively to the spherical disruptions and minute tubules found in the walls of many trepostome Bryozoa. **Endozone** and **exozone** are used as BOARDMAN (1959) defined them for contrasted inner and outer parts of zoaria as illustrated in Figure 2.

A somewhat unconventional practice is employed in indicating various directions within a zoarium (Fig. 2). **Distal** and **proximal** are used to refer only to the directions of endozonal expansion, that is, denoting only radius vectors of encrusting zoaria and vectors of branch extension of ramose zoaria. **Anterior** and **posterior** refer to directions along axes of the zooecia, as used in a similar way for cyclostomes by BRIEN (1960). Thus, the aperture of a zooecium is considered to be at its anterior end, and each zooecium has a distal side, a proximal side, and two lateral sides. Under terminology more widely used, distal and proximal refer to both vectors of zoarial growth

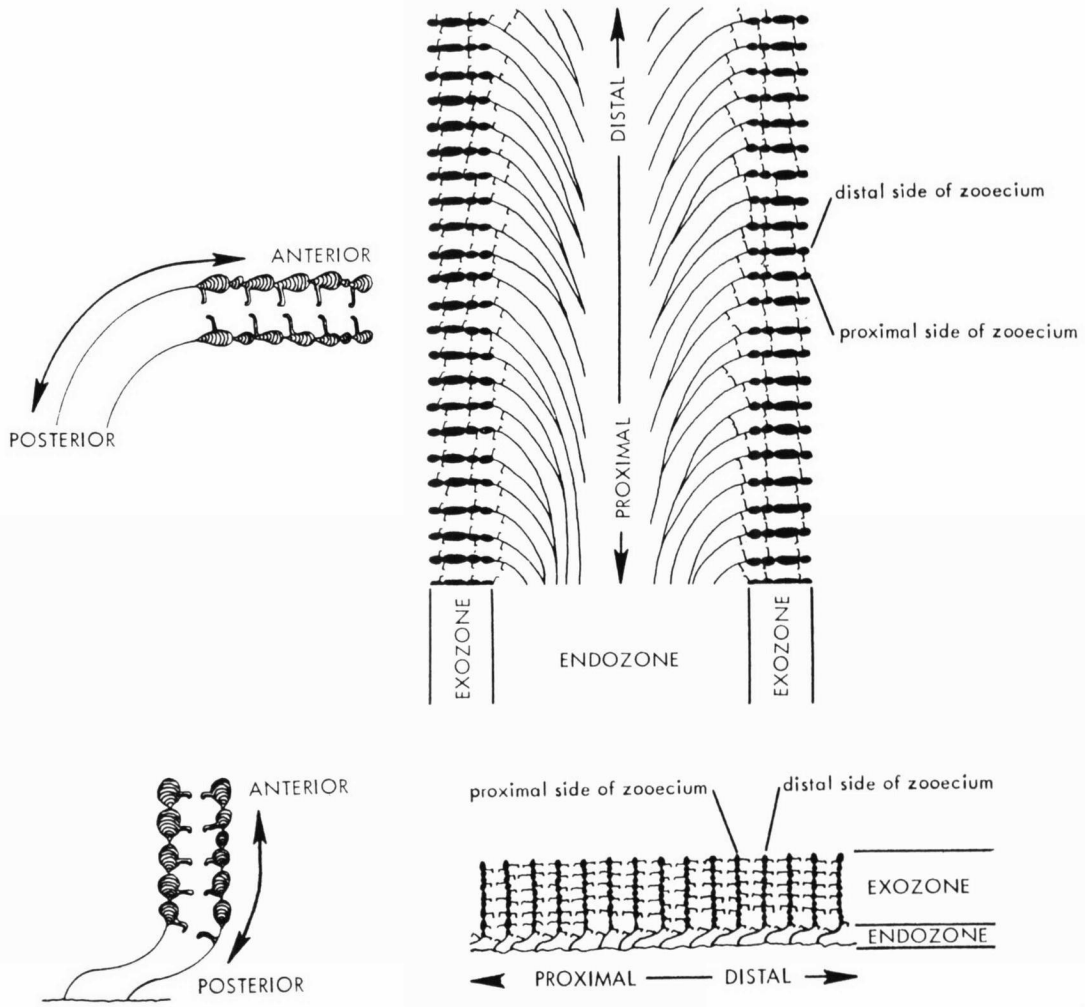


FIG. 2. Longitudinal sections (diagrammatic) showing endozone, and exozone regions, distal, proximal, anterior, and posterior directions in ramose and encrusting zoaria of trepostome Bryozoa.

and zooecial growth, so that a zooecium would have both distal and proximal ends, and distal and proximal sides. Under certain circumstances this terminology could cause confusion in descriptions, and therefore it is here discarded.

FORM, GROWTH, AND FUNCTION OF RING SEPTA

The zooecia of *Tabulipora* are characteristically subdivided by incomplete washerlike transverse partitions (Fig. 3; Pl. 1, fig. 1-2; Pl. 2, fig. 1-4; Pl. 3, fig. 2, 4; Pl. 4, fig. 2-3; Pl. 5, fig. 1, 3-4; Pl. 7, fig. 1b-e; Pl. 8, fig. 2), which have been called centrally perforate diaphragms or perforate diaphragms. In this paper, the term diaphragm is restricted to imperforate partitions; the type of perforated partition or septum seen in *Tabulipora* is given the term **ring septum** which was suggested by R. S. BOARDMAN (personal communication) as a replacement for ring diaphragm (GAUTIER, 1968). The term **foramen** refers to the perforation of a septum.

Ring septa are present in all species of this genus but are reported by CUFFEY (1967) to be absent in some fragments of *Tabulipora carbonaria* (WORTHEN, 1875) (see possible explanation in the section on wall structure and colony growth). Ring septa are sparse in the endozone of ramose forms, absent in the endozone of en-

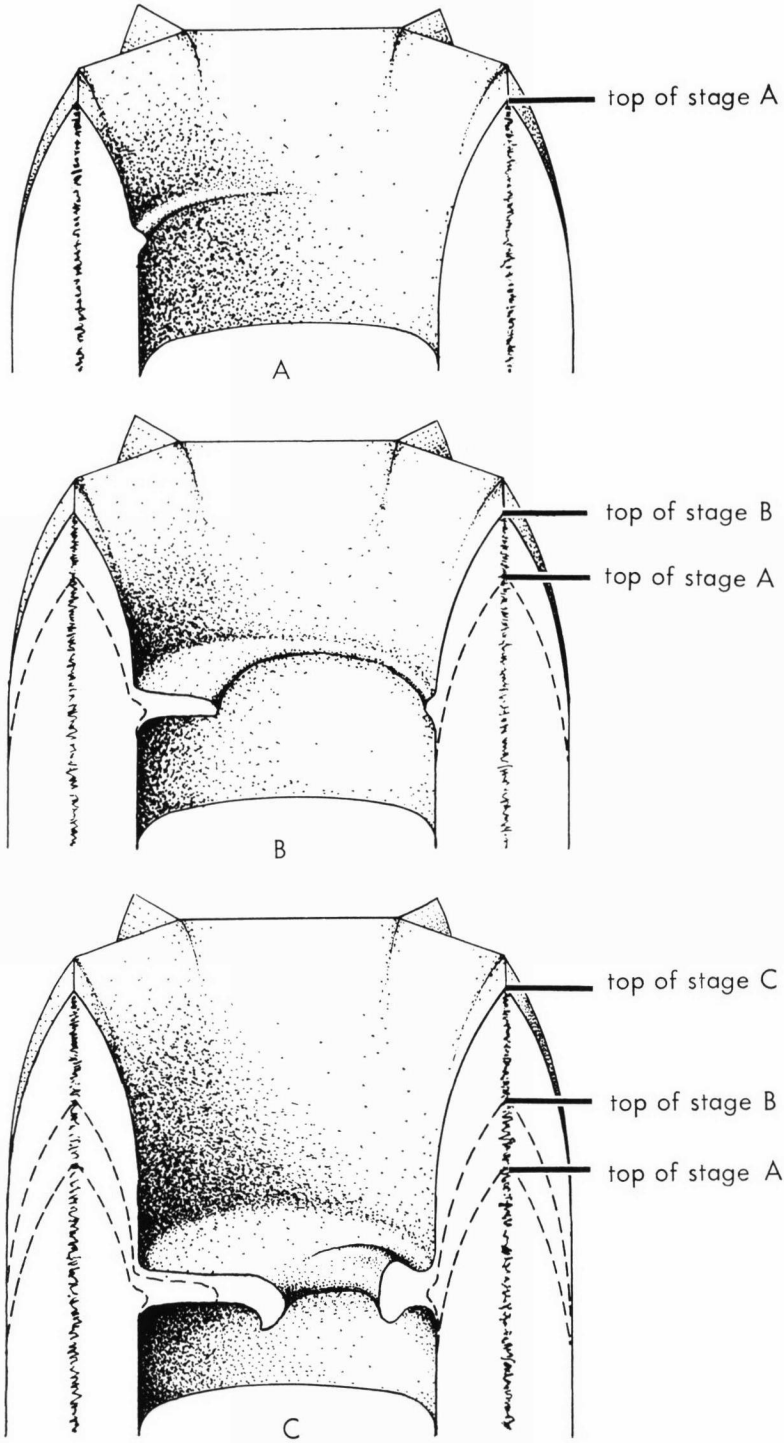


FIG. 3. Growth of tabuliporan ring septum indicated at selected successive stages *(A-C)* (diagrammatic).

crusting forms, but numerous in exozones of both. Endozone ring septa are thinner than exozone ring septa (Pl. 3, fig. 4). Ring septa are either perpendicular to the zooecial axes or are inclined a few degrees (Pl. 2, fig. 1; Pl. 5, fig. 1), usually with the distal side of the septum more posterior than the proximal side.

Microstructure of ring septa can be interpreted from their appearance in longitudinal, tangential, and transverse section (Pl. 1, fig. 1-2; Pl. 3, fig. 2; Pl. 8, fig. 2). The septa are made up of laminae

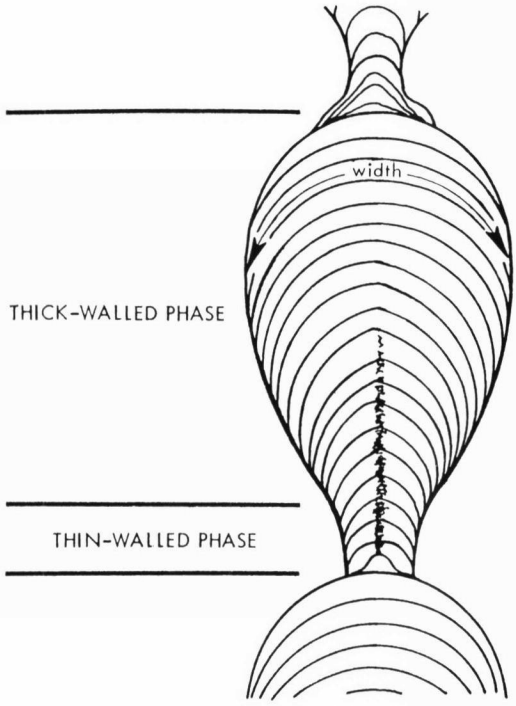


FIG. 4. Growth-cycle phases of paired annular thickenings in wall of tabuliporan zooecium (diagrammatic).

like those of the zooecial walls. Three zones roughly parallel to the surface of the septum can be distinguished on the basis of the character of the laminae (Pl. 1, fig. 1-2; Pl. 3, fig. 2). In the anterior zone, the laminae extend toward the foramen parallel to the surface or are slightly inclined posteriorly. The laminae nearest the zooecial wall in this zone are usually continuous with the wall laminae at least part way around the septum, whereas those on the more posterior edge of inclined septa may appear not to be. In the middle zone, the laminae of the anterior zone bend into the posterior zone, giving the laminae a V- or U-shaped appearance in section. The laminae of the posterior zone either terminate at the posterior surface of the septum or extend parallel to that surface back toward the zooecial wall where they lap posteriorly onto the wall forming a "bracket" (Pl. 1, fig. 1-2) and do not appear to be continuous with the wall laminae.

The anterior zone usually makes up most of the thickness of the septum, the middle zone being very thin, and the posterior zone thin or even absent. The middle zone usually appears as a dark line in sections, possibly because of optical effects produced by bending of the laminae. This dark line is an important characteristic since it can also be seen in sections which do not pass through the foramina (Pl. 3, fig. 2). In such cases, ring septa appear imperforate; but the dark line distinguishes them from diaphragms which are actually imperforate and lack the dark line because they were grown from the anterior side only.

The rims around the foramina are usually partly thickened and bent posteriorly, the deflection of the rim usually being continuous completely around the foramen. In addition, the segment of the rim on the flatter side of the foramen may be thickened by the addition of laminae on the anterior surface so that the rim is raised on that side in addition to being deflected posteriorly (Pl. 8, fig. 2). In *Tabulipora heteropora* (CONDRA, 1903) (Pl. 2, fig. 4) most rims are neither deflected nor thickened and appear blunt; but in an undescribed species from the Pennsylvanian of Texas (Pl. 2, fig. 1) the skeletal rings thin toward the foramina, the rims being more or less sharp.

The foramina may be kidney-shaped, oval, semielliptical, or circular; kidney-shaped foramina (Pl. 3, fig. 1; Pl. 7, fig. 1b-c) are by far the most common. The foramina in *Tabulipora urii* tend to be offset distally (Pl. 7, fig. 1b-c). This tendency can also be seen in most other species, and, as in *T. urii,* the straighter sides of the foramina are usually proximal.

The growth of ring septa is illustrated in Figure 3 and is discussed below.

Because the laminae of a ring septum are partially continuous with the wall laminae which arch over the zooecial boundary a short distance anteriorly into the adjacent zooecia, the ring septum must have formed near the aperture of

the zooecium which it divides. As the wall was being extended by addition of parallel layers of calcium carbonate, a transverse ridge was deposited at least part way around the zooecium near the aperture (Fig. 3,*A*). As the wall lengthened, the ridge was made wider by continued deposition of laminae around its inner margin (Fig. 3,*B*). Further deposition of progressively more extensive laminae thickened the skeletal ring and decreased the size of the foramen. Eventually the optimum foramen shape and size were approached, and wider laminae were deposited on the anterior surface causing the rim to curve posteriorly. At this time, additional deposition around the rim on the anterior surface produced a thickening on that side (Fig. 3,*C*). Growth halted when the proper foramen was formed.

Growth lines produced by this concentric growth of ring septa can be distinguished in some tangential sections intersecting the septa (Pl. 3,

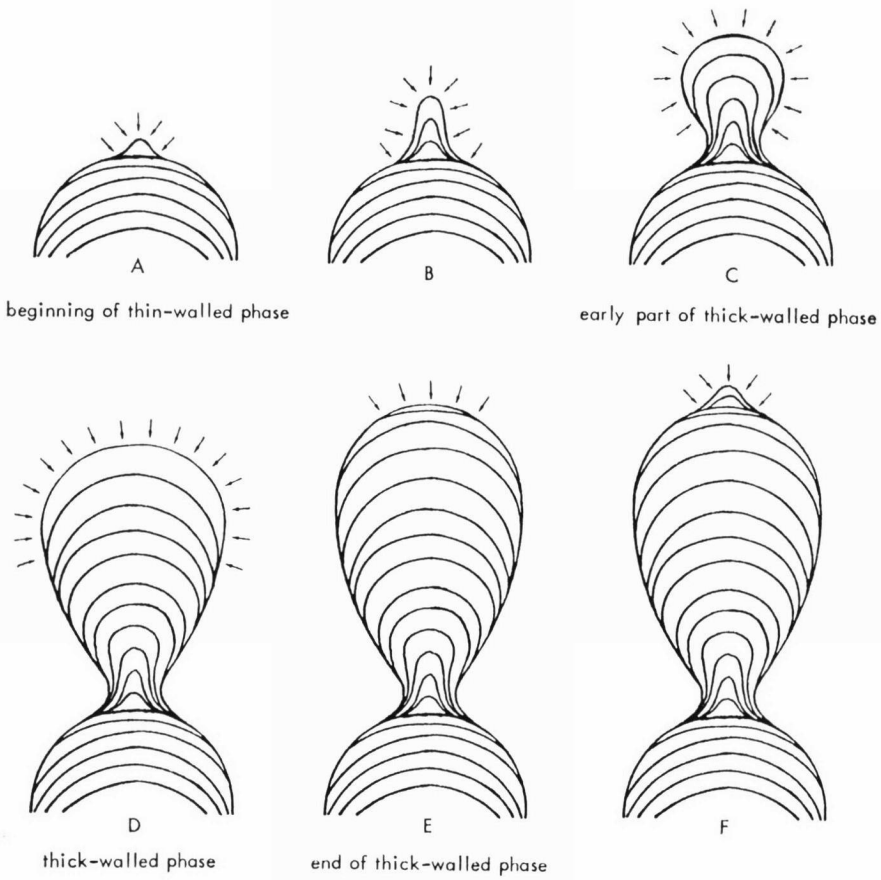
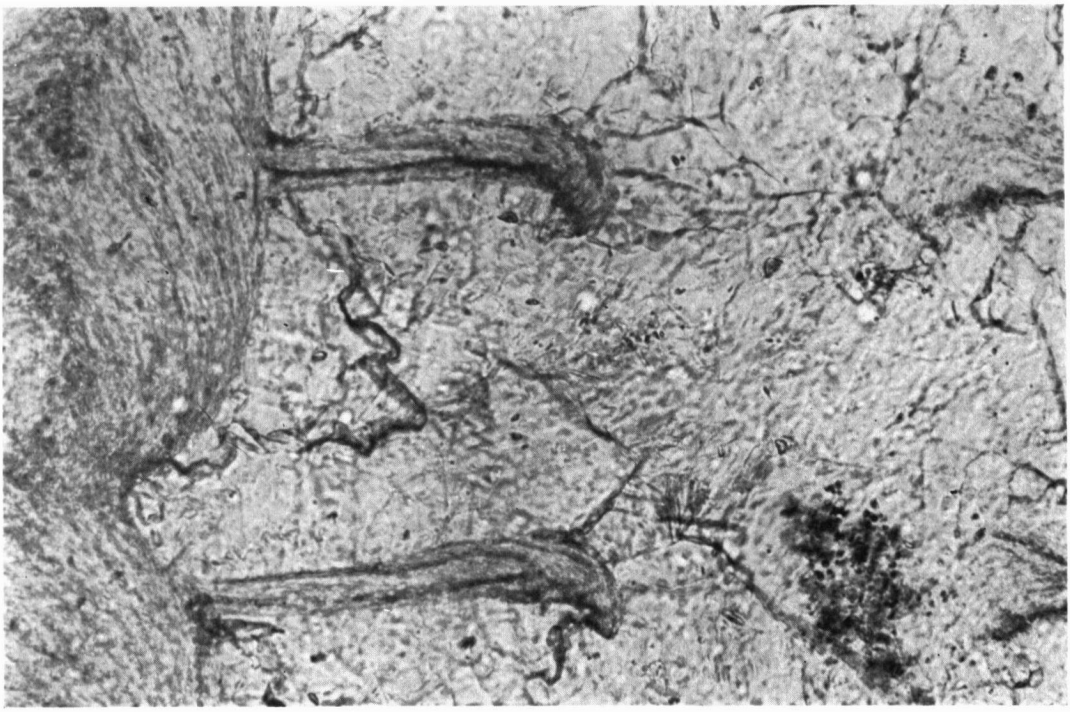


FIG. 5. Successive stages *(A-F)* in cyclic growth of beadlike section of two back-to-back annular thickenings in wall of tabuliporan zooecium (diagrammatic).

EXPLANATION OF PLATE 1

FIGURE

1. *Tabulipora ramosa* (ULRICH, 1890), USNM 164322, from Glen Dean Limestone, Upper Mississippian (Chesterian), Sloans Valley, Pulaski Co., Kentucky. Concentrically deposited laminae of distal portion of ring septum, central dark zone, posteriorly deflected foramina rims and anteriorly thickened proximal sides of foramina rims (barely visible on left), long. sec., ×485.
2. *Tabulipora* sp. A, USNM 164323, from Jacksboro Limestone, Upper Pennsylvanian (Ciscoan), Jacksboro, Jack Co., Texas (USNM loc. 14017). Ring septum structure, and darker material of diaphragm continuing anteriorly over zooecial walls and surface of ring septum, long. sec., ×500.



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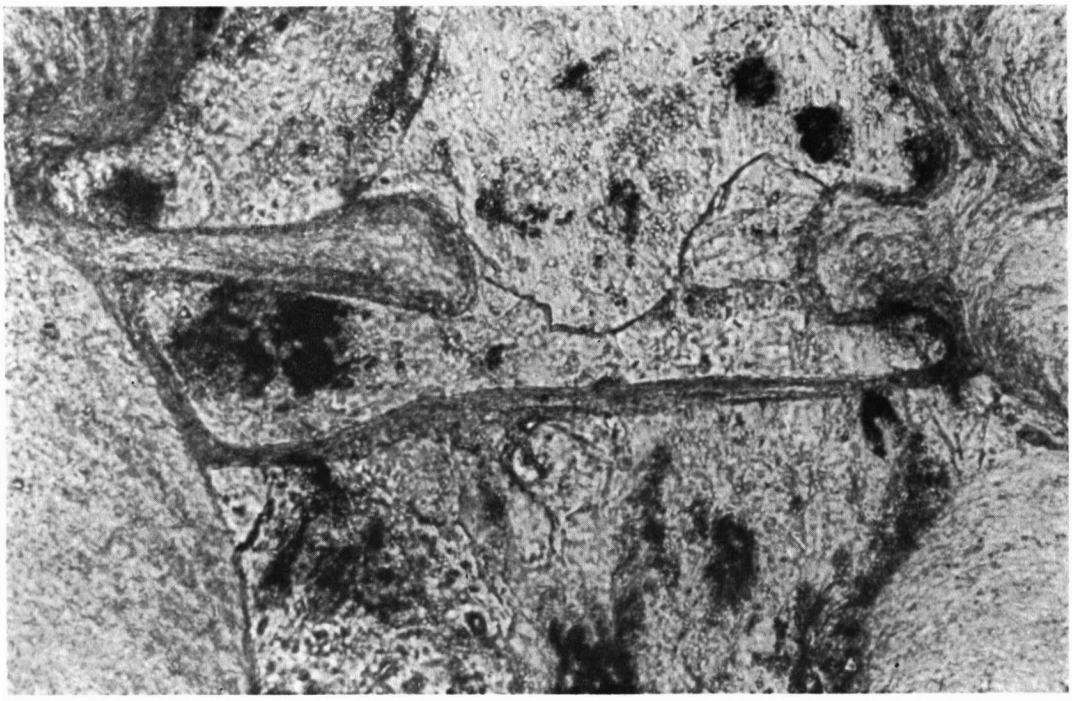

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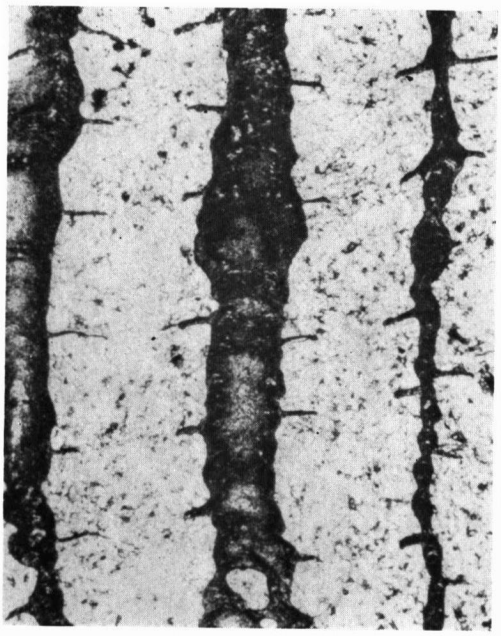

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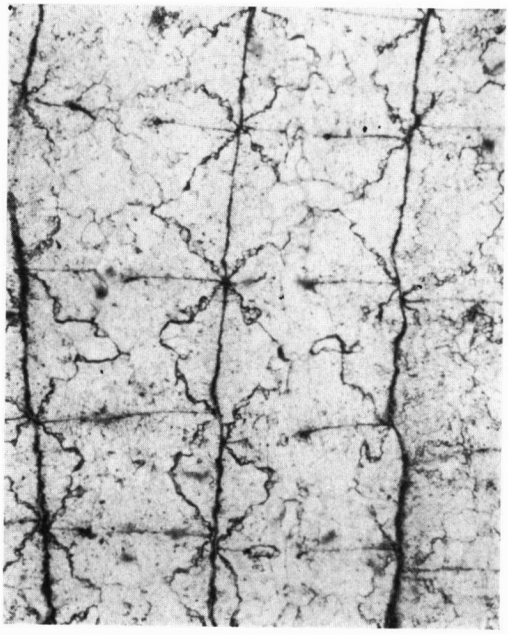

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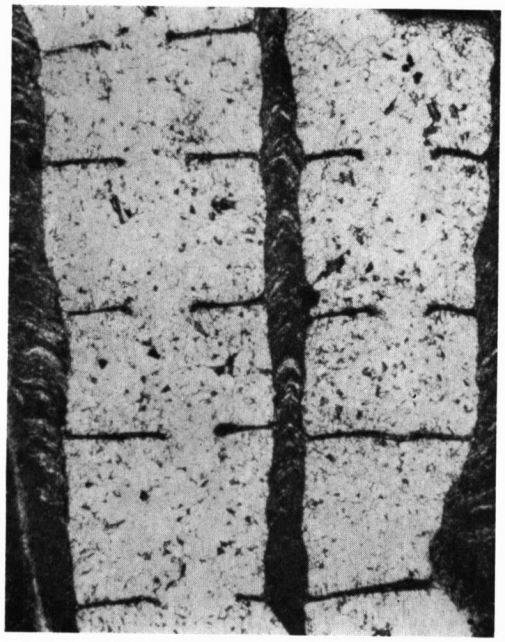

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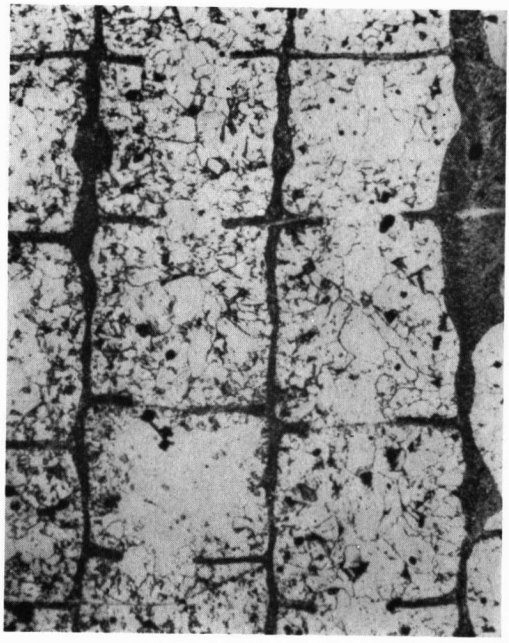

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fig. 1). When the foramina are offset, growth lines show that in their early stages of growth, ring septa had the form of hemiphragms or hemisepta, as described above (Fig. 3,*A*). In other cases a complete ring-shaped ridge was the earliest stage of growth. It is possible that sporadic hemiphragms reported in *Tabulipora carbonaria* by CUFFEY (1967) and seen in other species, could be early growth stages of ring septa. It is also possible that the foramina could be offset enough to form hemiphragms. Yet another possibility is evident in some species where the ring septa are at the same level as annular thickenings; the thickened walls restrict the zooecial cavities so much that the ring septa can hardly be detected, and they appear as hemiphragms if the foramina are offset. Since hemiphragms are almost negligible in number in *Tabulipora,* they are not regarded as distinguishing characters of the genus.

The initial position of ring septa near the apertures of the zooecia and the similar shapes and positions of the foramina suggest strongly that the ring septa formed the anterior walls of the living chambers and that the foramina served as openings through which the moveable soft parts extruded.

FORM, GROWTH, AND FUNCTION OF DIAPHRAGMS

Two types of transverse imperforate partitions occur in *Tabulipora*: 1) originally imperforate partitions stretching across the zooecia of some Pennsylvanian and Permian species, notably *T. carbonaria* (Pl. 1, fig. 2; Pl. 4, fig. 3; Pl. 5, fig. 3-4); 2) ring septa developed into imperforate partitions by deposition of a plate (foraminal plate) across the foramen (Pl. 2, fig. 4; Pl. 3, fig. 2; Pl. 4, fig. 3; Pl. 5, fig. 3). In this discussion, the term **diaphragm** refers only to the originally imperforate partitions, not the secondarily closed ring septa, although the latter probably served the same function.

Foraminal plates are thin structures which appear gray or very dark in thin sections. A gray foraminal plate is made up of laminae resembling those of the zooecial walls. These laminae are parallel to the surface of the plate, and at margins of the plate they lap onto the anterior surface of the ring septum but do not continue over the surface beyond the rim area. The darker foraminal plates seem to be similar in structure but apparently are less calcified and seem to contain a great amount of iron oxide, which may have resulted from chemical change of an original organic compound.

Diaphragms occur abundantly only in *Tabulipora carbonaria* and in an undescribed species of the genus from the Pennsylvanian of Texas. They are numerous in the endozones of these species and become more abundant in the exozones. Unlike the ring septa, diaphragms appear dark brown or black and the laminae are completely parallel to the surface of the diaphragm. The laminae lap anteriorly onto the zooecial walls and may continue along the wall to form a secondary zooecial lining (Pl. 1, fig. 2; Pl. 3, fig. 3). If a ring septum is present just anterior to a diaphragm, the secondary lining extending from the diaphragm may cover the surface of the septum (Pl. 1, fig. 2). In other cases the diaphragms are deposited on the anterior surfaces of the ring septa so that only one partition exists, rather than two (Pl. 5, fig. 2). By the continuation of their laminae over the whole anterior surface of the septum, these diaphragms can be distinguished from foraminal plates, whose deposits are restricted to the rim area.

EXPLANATION OF PLATE 2

FIGURE

1. *Tabulipora* sp. B, USNM 164324, from Millsap Lake Formation, Middle Pennsylvanian (Desmoinesian), Palo Pinto Co., Texas. Irregular zooecial walls and ring septa, some with sharp foramen rims, long. peel, ×75.
2. *Tabulipora tuberculata* (ULRICH, 1890), USNM 164325, from Mississippian near Cedar Bluff, Caldwell Co., Kentucky. Very thin zooecial walls, long. sec., ×75.
3. *Tabulipora heteropora* (CONDRA, 1903), KU25014a, from Pennsylvanian near Vilas, Wilson Co., Kansas. Thick irregular to even zooecial walls, long. peel, ×75.
4. *Tabulipora heteropora* (CONDRA, 1903), from Pennsylvanian, Riley Co., Kansas. Irregular to annularly thickened walls, ring septa without thickened or deflected foramen rims, and foraminal plates, long. peel, ×75.

Diaphragms may be slightly calcified, but their dark brown or black color suggests that they consist mainly of iron oxide. This may have resulted from alteration of a great amount of organic matter, as in the foraminal plates. The supposed organic composition of these structures may account for their lack of preservation in most species of *Tabulipora*. The conditions at the site of burial and the nature of fossilization probably were not conducive to the preservation of these structures in most forms.

Diaphragms and foraminal plates were deposited wholly by tissue on their anterior sides, as is indicated by the complete lack of laminae lapping posteriorly onto the zooecial walls or ring septa. It seems likely that no living tissue was present on the posterior side of these diaphragms, because there would have been no means of nourishment for such tissue. Diaphragms are formed in the zooecia only a few zooecial diameters within the tubes and all tubes contain them. Therefore, most of the bulk of the zoarium, i.e., the part on the proximal side of the diaphragms, must have lacked soft living tissue, the living matter covering only the periphery.

In the many specimens examined it is evident that no diaphragms or foraminal plates were formed beyond the most anterior ring septa. Usually they were formed posterior to two or three ring septa. Although no measurements were made, the distance between the last diaphragms and the most anterior ring septa appears to be nearly constant, varying only by one or two zooecial diameters. In some specimens (Pl. 4, fig. 3; Pl. 5, fig. 4) the formation position of diaphragms seems to depend partly on the position of ring septa. Thus, it is apparent that the diaphragms formed the posterior walls of the living chambers, the ring septa being the anterior walls, and that the living chambers were of similar size or volume. The implications of this condition in these fossil Bryozoa are great. Knowing the volume of the living chambers one could deduce the approximate size of the polypides, and perhaps learn the variations between older and younger parts of the zoaria, and between zoaria.

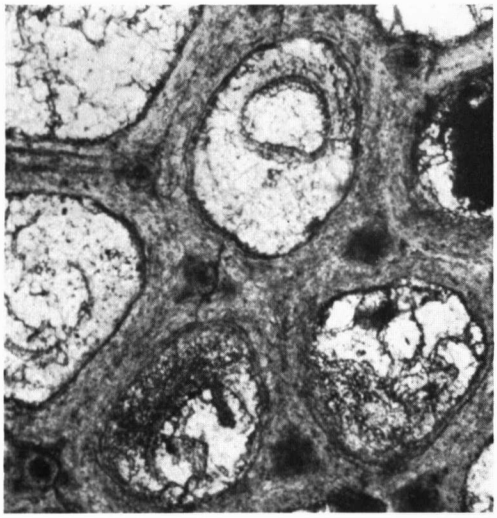
WALL STRUCTURE AND COLONY GROWTH

Zooecial wall structure is important in differentiating species of *Tabulipora,* as well as distinguishing this genus from others. Wall structure also provides a zoarial growth record unequalled, so far as known, in trepostomes other than the stenoporids. Like those of most trepostomes, a *Tabulipora* zoarium can be divided into two regions—endozone and exozone. Endozone zooecial walls are characteristically thin, but they may be thickened along the traces of abandoned growing tips (Boardman, 1960), arching distally from the base of the exozone into the endozone (Pl. 4, fig. 3; Pl. 5, fig. 3-4; Pl. 6, fig. 1a-e). Exozone zooecial walls in a few species may be no thicker than those of the endozone (Pl. 2, fig. 2; Pl. 4, fig. 2), but in most they are either slightly thicker and uneven (Pl. 2, fig. 1, 3-4) or are periodically greatly thickened in short segments separated by thin walls (Fig. 6; Pl. 5, fig. 1-4; Pl. 6, fig. 1a, 1c-e; Pl. 7, fig. 1d-e). The periodically thickened walls have been conveniently described as beaded, or moniliform, because of their appearance in sections. Each bead is made up of a posterior thin-walled phase in which the V-shaped laminae are narrow, and an anterior thick-walled phase in which they are wide (Fig. 4).

EXPLANATION OF PLATE 3

Figure

1. *Tabulipora ramosa* (Ulrich, 1890), USNM 164326, from Mississippian, Falls of the Rough, Grayson Co., Kentucky (USNM loc. 14028). Ring septum with growth line on proximal side defining earlier hemiphragm stage of growth, tang. sec., ×100.
2. *Tabulipora tuberculata* (Ulrich, 1890), USNM 164327, from Glen Dean Limestone, Upper Mississippian (Chesterian), Sloans Valley, Pulaski Co., Kentucky. Dark zones of ring septa and ring septum with foraminal plate supporting sediment, long. sec., ×100.
3. *Tabulipora* sp. A, USNM 164323, from Jacksboro Limestone, Upper Pennsylvanian (Ciscoan), Jacksboro, Jack Co., Texas (USNM loc. 14017). Zooecial lining of dark material continuous with material of diaphragm deposited on anterior surface of ring septum, long. sec., ×400.
4. *Tabulipora ramosa* (Ulrich, 1890), USNM 164328, from Glen Dean Limestone, Upper Mississippian (Chesterian), Breckenridge Co., Kentucky (USNM loc. 14046). Thick ring septa in exozone, thin ring septa in endozone, and interzooecial layer of annular thickenings in endozone, long. peel, ×50.



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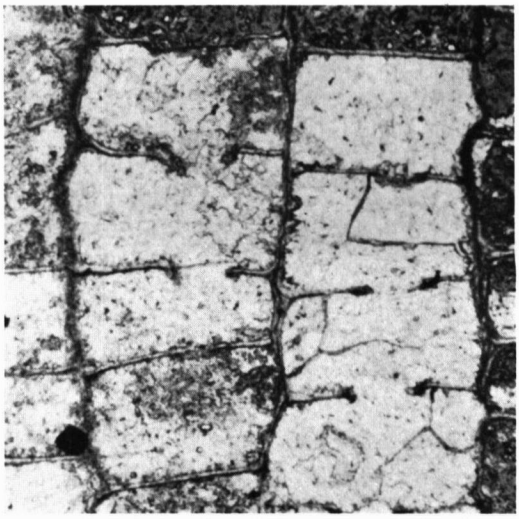

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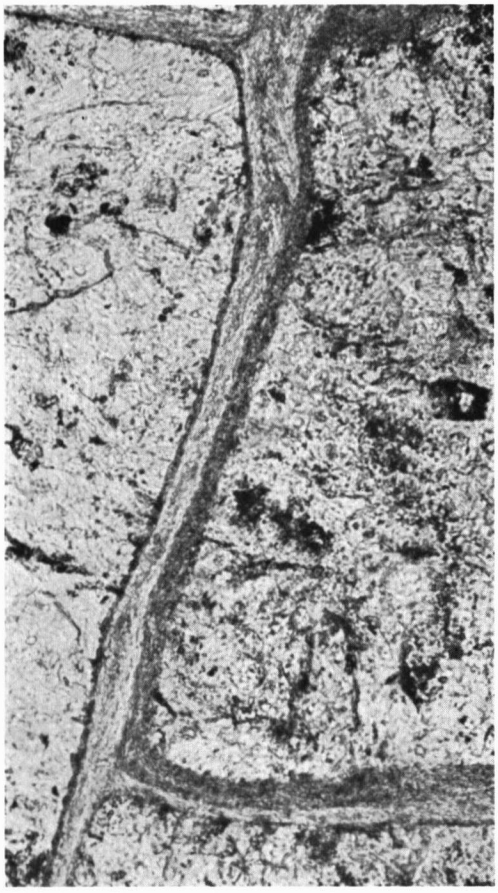

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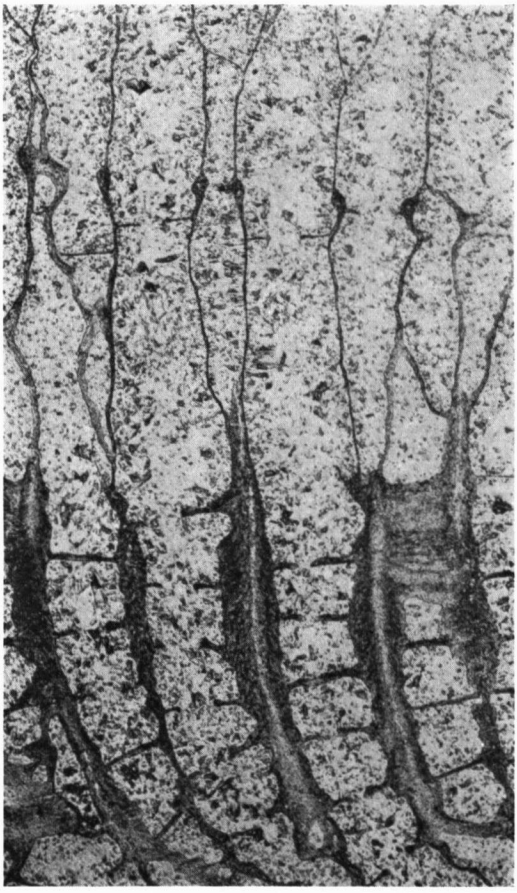

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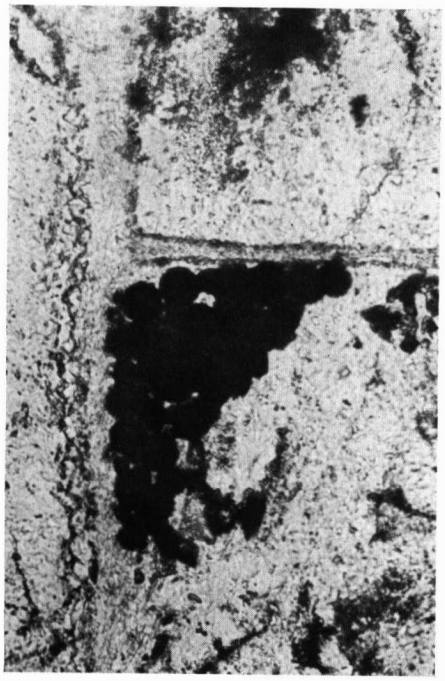

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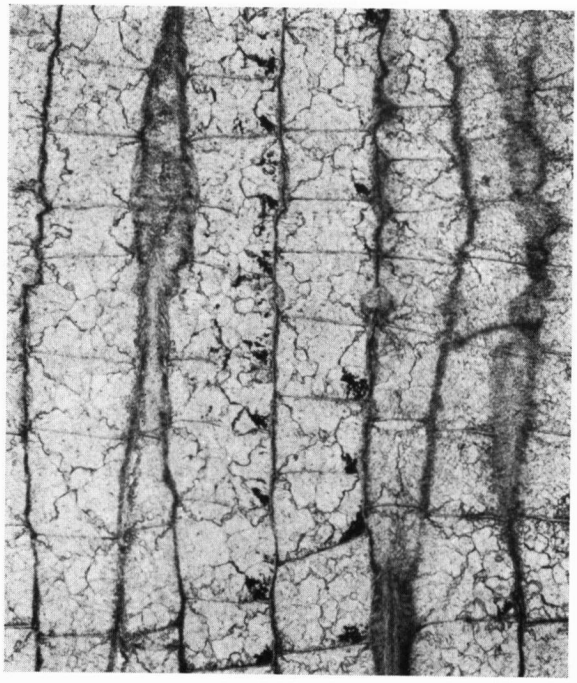

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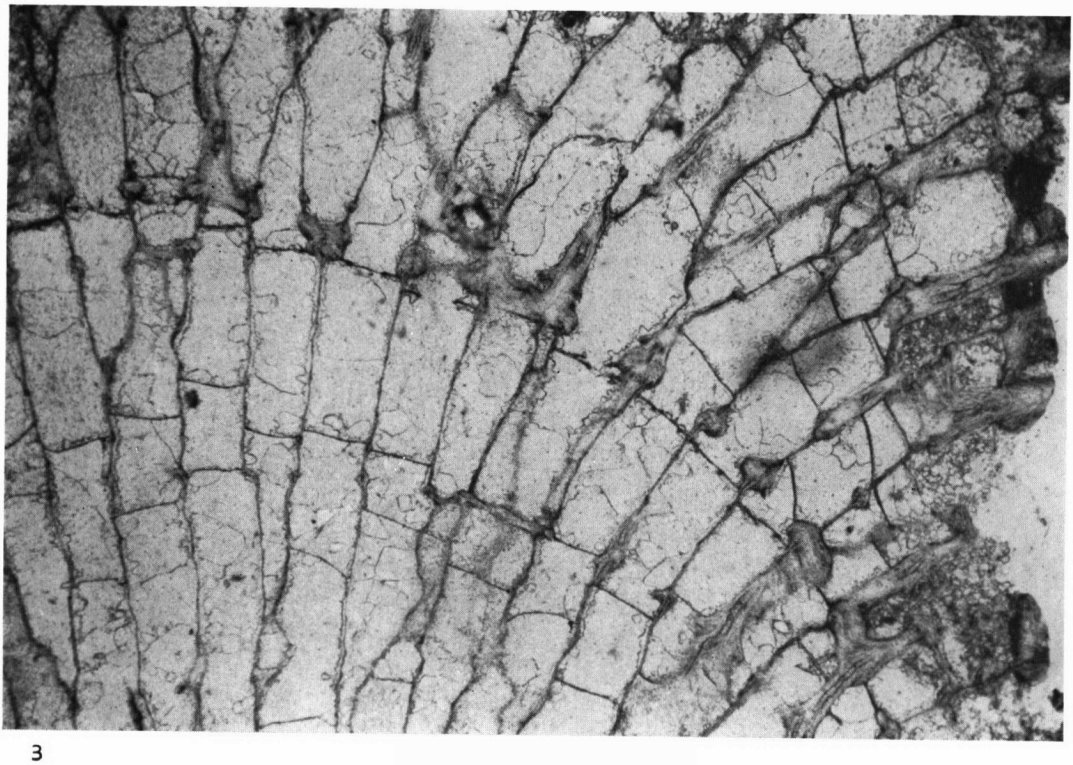


3

A bead is a section of two back-to-back annular thickenings, each completely encircling its own zooecium (Fig. 6; Pl. 7, fig. 1b). In *Tabulipora carbonaria* and other species with well-developed annual thickenings, the thickenings are cyclic and aligned from zooecium to zooecium so that in sections these thickenings appear as rows of beads that parallel zoarial surfaces (Fig. 6; Pl. 4, fig. 3; Pl. 5, fig. 1-4; Pl. 6, fig. 1a, 1c-e; Pl. 7, fig. 1d-e). These are here called **interzooecial layers** of annular thickenings, or just layers.

These closely spaced exozonal layers are continuations of layers in the abandoned growing tips of the endozone. The endozone layers are more numerous, groups of them merging in the outer endozone to continue proximally as a single exozone layer (Fig. 7a, c-d; Pl. 5, fig. 1a, c-d), but their thick-walled phases are usually much more widely spaced due to lengthening of the thin-walled phases which form most of the length of the endozone zooecial walls. At wide intervals along the branches some layers completely cross the endozone. Between these are other layers in which the thick-walled phases can only be traced in the outer endozone, the axial portions of the layers being merely slight disruptions in the thin zooecial walls (Pl. 5, fig. 1b-c).

Parallelism between the surface of the zoarium and the exozone layers and similarity in the shapes and sizes of the beads in any one layer leave little doubt that the layers are zoarial growth increments. The expression of the increments as alternating thin and thick walls indicates that colony growth was cyclic, resulting in alternate increases and decreases in the total area of epithelium-depositing skeletal material on the zoarium. This phenomenon is illustrated in Figure 5, which shows that the narrower laminae of the initial thin-walled phase were deposited by a narrow portion of the epithelium. As the cycle of growth continued, the band of deposition widened, increasing the width of the laminae and thus local thickness of the wall.

The above relationships provide information about the pattern and relative rate of branch extension. In Figure 7, since exozone layer *C* is a growth increment, its endozonal extensions, layers *C,1-5,* were deposited during the same time interval. Because the endozone zooecial walls are longer than the corresponding exozone walls, the endozone walls must have grown at a more rapid rate; and since only the thin-walled phases of these endozonal layers are lengthened, they—not the thick-walled phases—must represent the periods of rapid growth. Furthermore, the rate of growth of the thin walls decreased toward the exozone, in which direction they become shorter, most of them disappearing where their bracketing thick-walled phases merge together. This decrease in growth rate continued proximally in the exozone where exozone layers can also be seen to merge together (Figs. 7a,e; Pl. 6, fig. 1a,e).

It cannot be said whether total $CaCO_3$ uptake by the colony increased, decreased, or remained constant when the branch extension entered the rapid-growth thin-walled phase. The only requirement this phase would have imposed upon the colony is that the depositing tissue increase its rate of deposition in the areas of thin-walled growth. The decrease in total area of deposition accompanying the onset of thin-walled growth would have decreased the amount of $CaCO_3$ needed to sustain a slow rate of extension. Any increase over this minimum amount of required $CaCO_3$, even to a level less than the amount deposited during a thick-walled phase, would have allowed the rate of branch extension to increase. It is possible that owing to slower growth rate of thin

EXPLANATION OF PLATE 4

FIGURE

1. *Tabulipora* sp. A, USNM 164323, from Jacksboro Limestone, Upper Pennsylvanian (Ciscoan), Jacksboro, Jack Co., Texas (USNM loc. 14017). Brown bodies piled against posterior distal side of ring septum, long. sec., ×400.
2. *Tabulipora cestriensis* (ULRICH, 1890), USNM 164329, from Mississippian (Middle Chester), Caldwell Co., Kentucky. Brown bodies piled against anterior proximal sides of ring septa, long. sec., ×50.
3. *Tabulipora carbonaria* (WORTHEN, 1875), USNM 164330, from Wabaunsee Group, Upper Pennsylvanian (Virgilian), Dunbar, Otoe Co., Nebraska (USNM loc. 14037). Endozone interzooecial layers of annular thickenings with ring septa, foraminal plates, and diaphragms forming posterior walls of living chambers of similar size, long. sec., ×35.

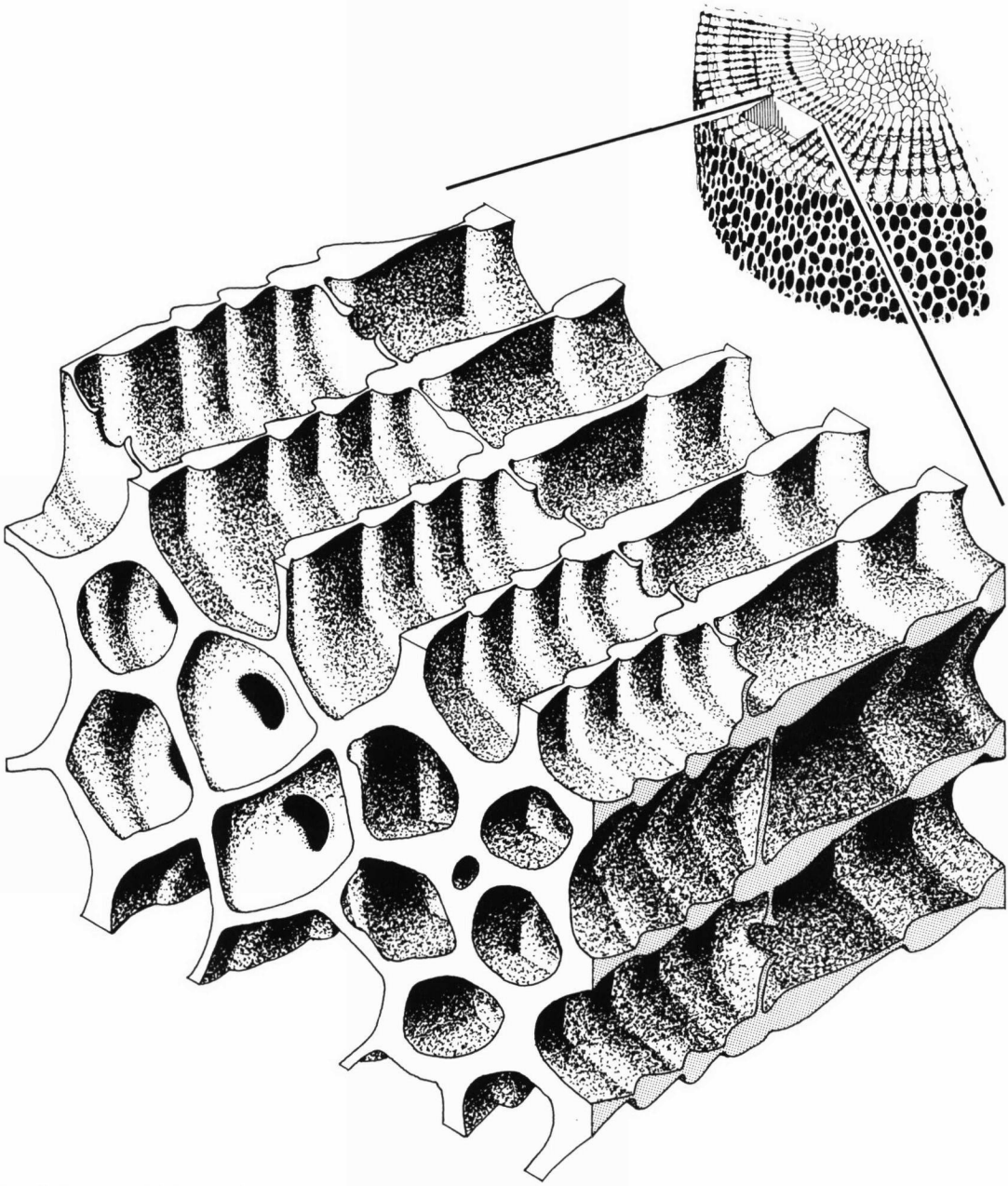


FIG. 6. Interzooecial layers of annular thickenings representing zoarial cycles of growth in *Tabulipora* (diagrammatic).

walls farther from the axis of the branch, the amount of $CaCO_3$ deposited in units of time increased near the axis and decreased near the exozone. Thus, the cyclic growth in *Tabulipora* may not have been due to fluctuations in capacity of the colony to deposit skeletal tissue.

Cyclic zoarial growth also influenced the positions of the ring septa. This is clearest in the endozone where the ring septa, when present, are restricted to the annular thickenings (Pl. 4, fig. 3; Pl. 5, fig. 4; Pl. 6, fig. 1a,c-e). In the exozones of some specimens (Pl. 6, fig. 1a), ring septa also form interzooecial layers which are more or less regularly spaced, but at wider intervals than the

annular thickenings. CUFFEY (1967) reported finding fragments of *Tabulipora carbonaria* which contained no ring septa, but this does not necessarily mean that the whole zoarium lacked ring septa. For instance, a specimen here illustrated (Pl. 5, fig. 4) would not have had ring septa, but would still have had an exozone if the colony had died before formation of the ring septa seen in the outer part of the existing exozone.

If ring septa were a structure necessary for the operations of polypides, then they may not have functioned at tips of branches during rapid thin-walled phases of growth during which time ring septa were not formed in the endozone. If this assumption is correct, the growth of ring septa in the thick-walled phases of the endozone would indicate that polypides were present then. This is one line of evidence for suggesting that some soft parts of *Tabulipora* polypides underwent degeneration and regeneration, but more convincing evidence is the presence of brown bodies in the zooecia (Pl. 4, fig. 1-2). These are particles that resemble degeneration products in Recent Bryozoa, and CUMINGS (1915) suggested that they were the same. Brown bodies were definitely present in the zooecia of *Tabulipora* prior to filling of the tubes with calcite, because they form geopedal structures (Pl. 4, fig. 1-2).

Therefore, cyclic zoarial growth exhibited by species of *Tabulipora* may have been in some way associated with the degeneration and regeneration of soft parts. The lack of ring septa in some endozone thick-walled phases might indicate that soft parts did not always regenerate at those times at branch tips. Slowing of branch extension may have occurred simultaneously with regenerations in the exozone, not necessarily accompanied by regenerations in the endozone. On the other hand, cyclic slowing of branch extension may have been a response to environmental influences; sometimes the thick-walled phases may not have lasted long enough to permit regeneration in the endozone. A further suggestion (R. S. BOARDMAN, personal communication) is that resorption removed some structures from the endozone. It should be noted that most endozonal layers, complete or incomplete in the axial region, contain ring septa in the outermost endozone where branch extension was slower.

In summary, referring to Figure 7 and Plate 6, growth of branch segment *C* is judged to have occurred in the following steps:

1) Thick-walled phase *B,25* ended with degeneration of polypides in the exozone and endozone, and the beginning of thin-walled growth which was more rapid in the endozone.
2) Thin-walled growth slowed in the endozone and exozone, and the slow growth of thick-walled layer *C,1* began along with its corresponding portion of exozone layer *C*.
3) Ring septa and diaphragms grew in the outer endozone; soft parts regenerated and polypides became functional in new living chambers of the outer endozone and old living chambers of the exozone.
4) Steps 1-3 were repeated four times with minor variations, but without thin-walled growth in the exozone.
5) Thick-walled phase *C,5* ended with degeneration, and the beginning of thin-walled growth in the endozone and part of the exozone.

EVOLUTIONARY TRENDS IN TABULIPORA

During the course of this revision, specimens of many North American species have been examined, with notice of more distinct variations and trends in the genus through the Mississippian, Pennsylvanian, and Permian periods. Worldwide trends are not discussed here because too few specimens from outside of North America have been available for study.

North American species of *Tabulipora* fall into two stratigraphic groups, one from Mississippian deposits and the other from Pennsylvanian and Permian sources. The only Mississippian species known to continue into the Pennsylvanian is *T. tuberculata* (PROUT, 1859), specimens of which were found in the University of Kansas Museum of Invertebrate Paleontology collection from the McCoy Formation of Colorado. CUFFEY (1967) has pointed out that the Mississippian *T. ramosa* (ULRICH, 1890)-*T. cestriensis* (ULRICH, 1890) complex apparently gave rise to *T. carbonaria* (WORTHEN, 1875) and related forms in the Pennsylvanian and Permian. Evolutionary trends can be shown in and between these two groups.

A tendency for zooecial walls of *Tabulipora* to increase in thickness from the Mississippian to the Permian has been noted by other authors (CUFFEY, 1967; DUNAEVA & MOROZOVA, 1967) and is illustrated in Figure 8, a histogram of average maximum wall thickness in various North American species. The histogram indicates the existence of considerable overlap between species of the Mississippian and Pennsylvanian-Permian groups but that the range of the latter shifted toward greater thicknesses. This trend toward thickening of the zooecial walls seems to be connected with a general increase in the occurrence and organization of annular thickenings. In Mississippian species with thin zooecial walls (e.g., *T. tuberculata,* Pl. 2, fig. 2; Pl. 3, fig. 2; and *T. cestriensis,* Pl. 4, fig. 2), only the points of attachment of ring septa commonly are thickened, whereas in the thicker-walled Mississippian species (e.g., *T. ramosa,* Pl. 3, fig. 4; and *T. americana* (ULRICH, 1890), Pl. 5, fig. 1), well-developed annular thickenings occur. In thinner-walled Pennsylvanian and Permian species (e.g., *T. heteropora,* Pl. 2, fig. 3-4; and *T.* sp. B, Pl. 2, fig. 1) the annular thickenings are very irregular, if present at all; but in thicker-walled forms (e.g., *T. carbonaria,* Pl. 2, fig. 1a-e; Pl. 4, fig. 3; Pl. 5, fig. 3-4; and *T.* sp. A, Pl. 5, fig. 2), they are very well developed. Furthermore, the annular thickenings of the Pennsylvanian and Permian species are more regular in shape, and occur more constantly in one zoarium than those of the

EXPLANATION OF PLATE 5

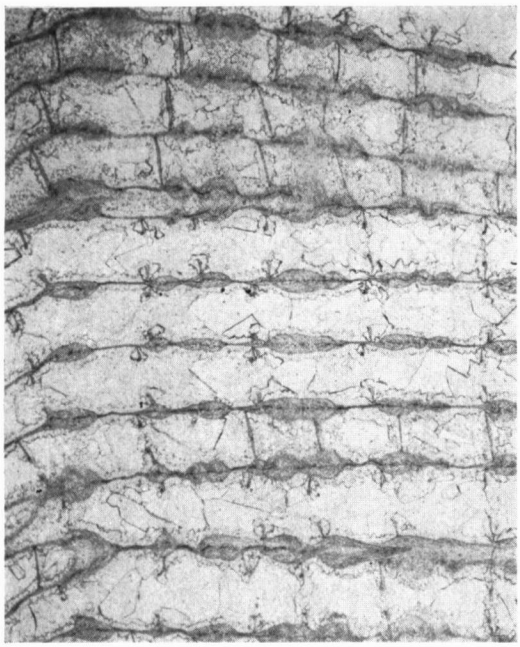
FIGURE

1. *Tabulipora americana* (ULRICH, 1890), USNM 164331, from Keokuk Limestone, Mississippian (Osagean), Warsaw, Hancock Co., Illinois. Interzooecial layers of annular thickenings and ring septa inclined distally especially at base of exozone at left of photo, long. sec., ×30.
2. *Tabulipora* sp. A, USNM 164323, from Jacksboro Limestone, Upper Pennsylvanian (Ciscoan), Jacksboro, Jack Co., Texas (USNM loc. 14017). Large, round and oval annular thickenings, ring septa, and zooecial linings, long. sec., ×100.
3. *Tabulipora carbonaria* (WORTHEN, 1875), USNM 164332, from Cisco Group, Upper Pennsylvanian (Virgilian), Cisco, Eastland Co., Texas (USNM loc. 14016). Endozone interzooecial layers of annular thickenings joining near base of exozone, and ring septa, diaphragms and foraminal plates in endozone and exozone, long. sec., ×30.
4. *Tabulipora carbonaria* (WORTHEN, 1875), KU26147a, from Eiss Limestone, Permian (Wolfcampian), northwest of Strong City, Chase Co., Kansas (KU loc. 9007). Interzooecial layers of annular thickenings, and two sets of living chambers defined by the two rows of diaphragms near the base of the exozone, and the two rows of ring septa near the surface, long. peel, ×30.

EXPLANATION OF PLATE 6

FIGURE

1. *Tabulipora carbonaria* (WORTHEN, 1875), KU26184a, from Camp Colorado Limestone, Pueblo Formation, Permian (Wolfcampian), Coleman, Coleman Co., Texas. [Letters referred to in this plate description are explained in the text and are illustrated in text Figure 7, a schematic tracing of interzooecial layers of annular thickenings shown in the plate figures.]——1a. Layer A is shown by two pointed indicators in exozone near bottom of photograph. The last-formed endozone layer of the unlettered sequence of layers beneath layer A, and those of layers A-D are shown by pointed indicators in the endozone. The boxes give the positions of Fig. 1b-e, ×7.——1b. Pointed indicators designate endozone layer of annular thickenings pinching out toward center of branch, ×20.——1c. Pointed indicator designates layer of annular thickenings shown in Fig. 1b as it approaches the exozone, ×20.——1d. The three pointed indicators at the top of the figure identify two endozone layers of group C and exozone layer D (right). The two endozone layers merge into one layer (left of middle two pointed indicators), then that layer merges with layer D (bottom pointed indicator), ×20.——1e. Pointed indicators show the merging of 3 exozone components of layer C (top 3 pointed indicators), merging into two, then one exozone layer (bottom pointed indicator), ×20.



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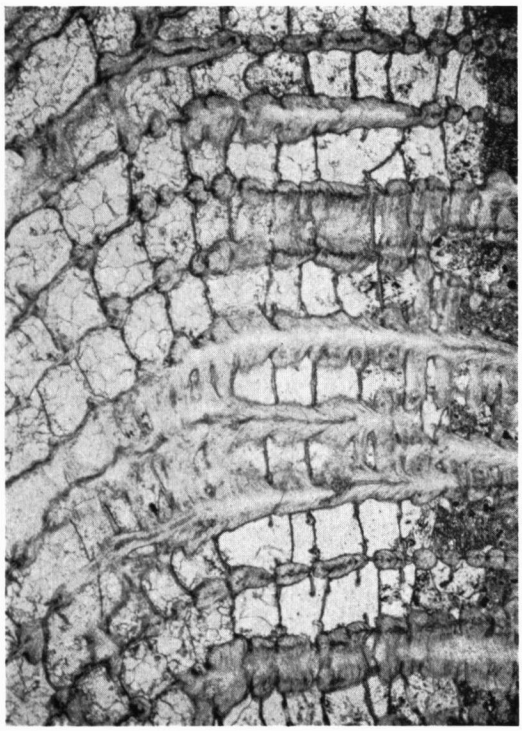

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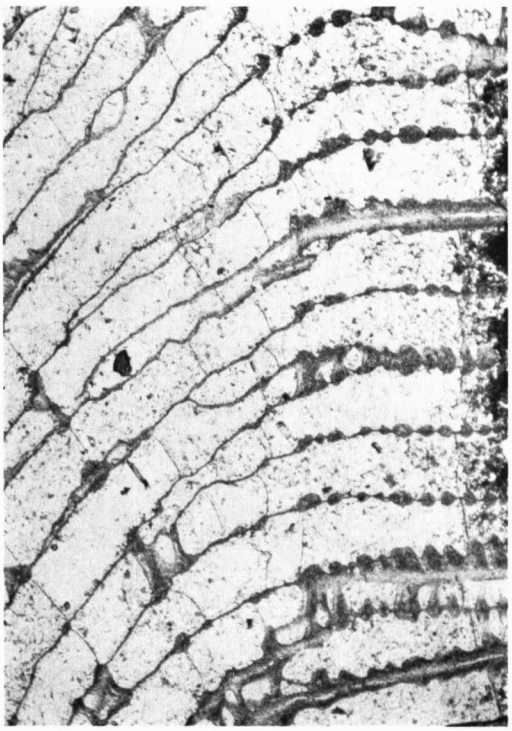

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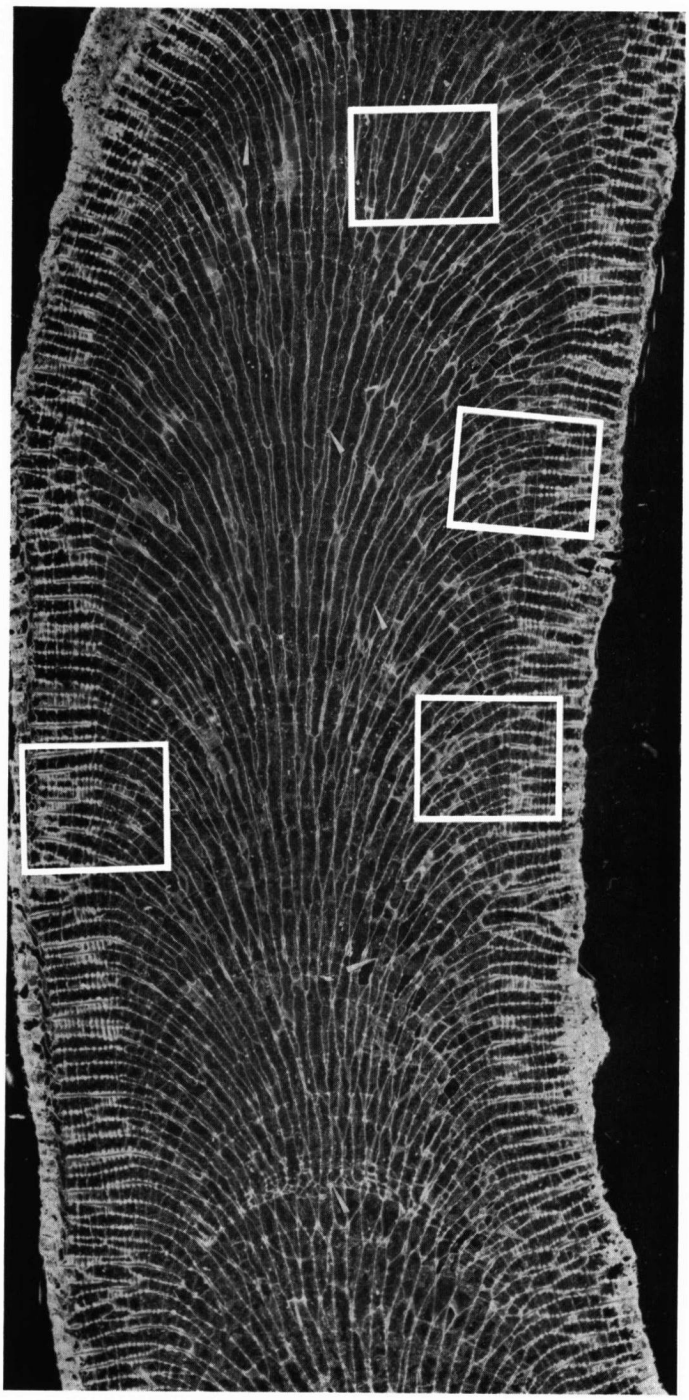

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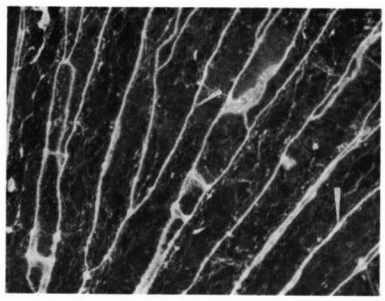

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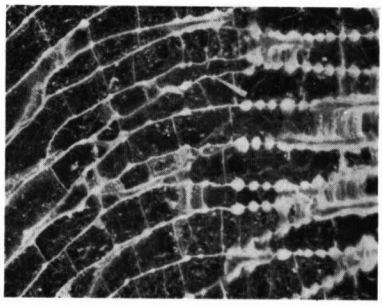

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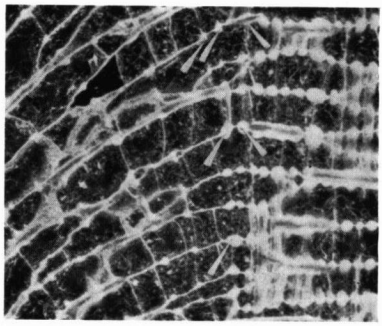

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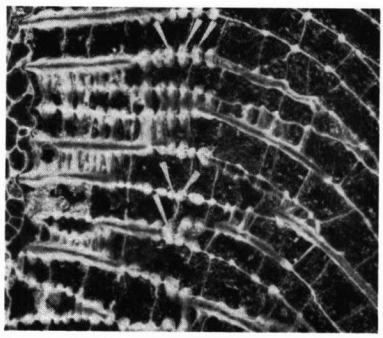


1e

(For explanation, *see* p. 14.)

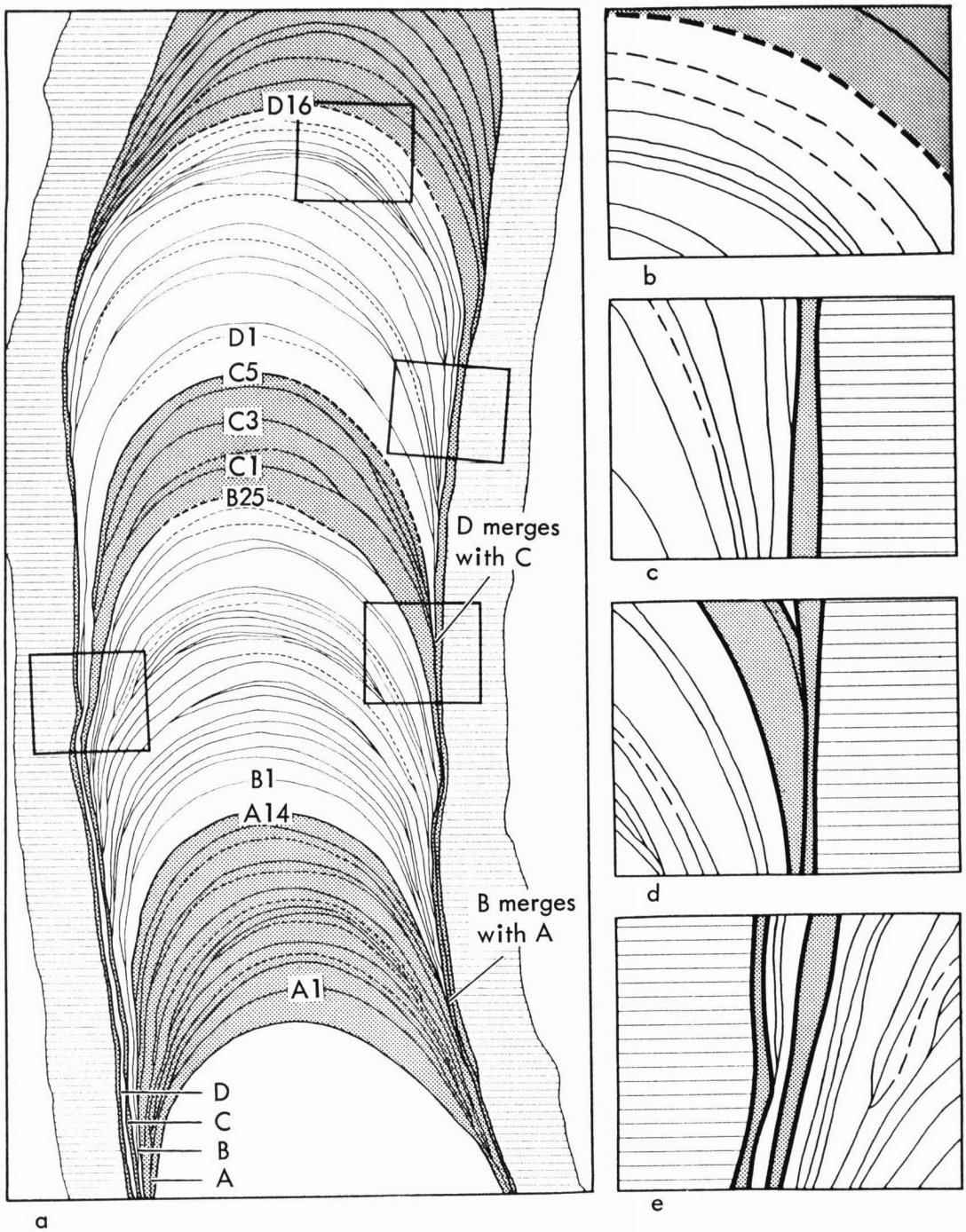


FIG. 7. Interzooecial layers of annular thickenings in peel of *Tabulipora carbonaria* shown in Plate 6.

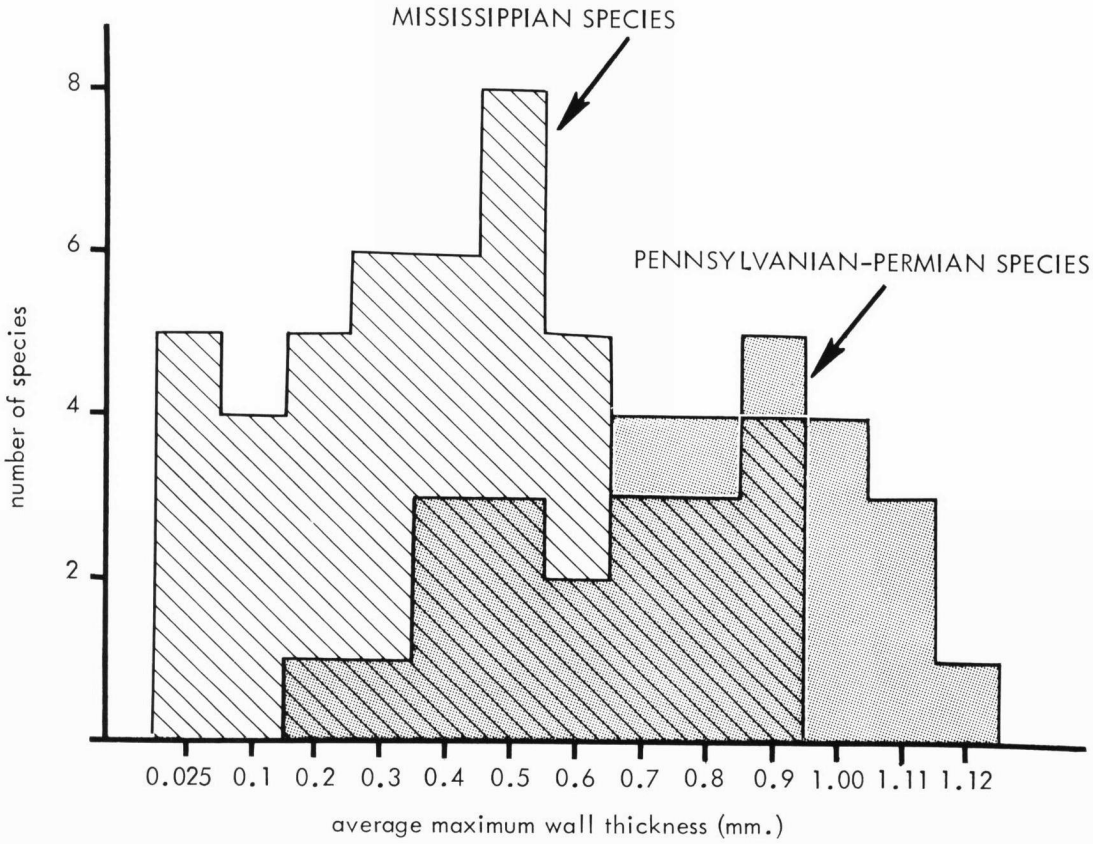


FIG. 8. Histogram of North American species of *Tabulipora* plotted against average maximum wall thickness (data from Gautier, 1968).

Mississippian species, which vary widely. This seems to indicate either that species with thicker walls were more affected by the conditions producing cyclic growth or that thicker walls were the result of developing cyclic growth, and that cyclic growth was more prevalent in the Pennsylvanian and Permian species than in those of the Mississippian.

The adaptive significance of thicker walls, especially annular thickenings, is unknown. Generally speaking, the thinner-walled forms have incrusting or massive zoaria, the ramose zoaria having thicker-walled zooecia; so a strengthening function of the thick walls seems probable. The annular thickenings might also have served to constrict the apertural opening for protection, or for other reasons.

Endozone layers of annular thickenings, endozone ring septa, and diaphragms are all structures which either make their first appearance in Pennsylvanian and Permian species, or are better developed in them than in Mississippian species. Diaphragms seem to have been largely made up of organic material, and may have been obliterated by fossilization of the Mississippian species, but the great abundance of these structures in the later species coupled with their virtual absence in the earlier ones, suggests that they never were present in the earlier ones. Ring septa develop in the endozone only in layers of annular thickenings; so when the endozone layers are absent or uncommon, as in *Tabulipora ramosa,* ring septa are similarly absent or uncommon. It is possible that resorption accounts for the lack of these structures in Mississippian species. This would mean that Pennsylvanian and Permian species had evolved to the point of not resorbing them. On the other hand, the Mississippian species may have lacked ring septa in the endozone, which might signify that no polypides existed there.

SYSTEMATIC DESCRIPTIONS

TABULIPORA Young, 1883

Monticulipora (Tabulipora) Young, 1883, p. 158.
Tabulipora Young, Etheridge, 1891, p. 47; Lee, 1912, p. 149-150, 162-176.
Amphiporella Girty, 1910, p. 199-200.
Sinotabulipora Yang, 1950, p. 8.

Type Species.—*Cellepora urii* Fleming, 1828 *(by monotypy)*.

Generic Definition.—Endozone-exozone boundary generally indistinct and irregular. Zooecia perpendicular to lateral surface of zoarium in well-developed portions of exozone. Zooecial walls in endozone commonly irregular, undulatory or crenulate; irregularly thick or thin in exozone or with annular thickenings, which may form interzooecial layers, closely spaced and parallel to lateral surface of branch; some may arch distally into endozone from base of exozone. Zooecial apertures usually arranged in irregular pattern.

Ring septa present in exozone of zoaria of all species; may be absent in some fragments; foramina usually with a major and minor axis, most offset distally. Many endozone zooecial corners occupied by tube without concentric laminae; tubes continuous with acanthopores in exozone or in layers of annular thickenings in endozone. Acanthopores may vary widely in number and position. Exilapores sparse to common, number varying widely within zoarium. Monticules composed of clusters of larger-than-normal zooecia, or smaller-than-normal zooecia; monticular zooecia with thinner or thicker walls than those of intermonticular zooecia.

Stratigraphic and Geographic Distribution.—Dev.-Perm., Russia; Miss.-Perm., N.Am.; Carboniferous, British Isles, China, Timor; Perm., Australia, Greenland, Japan, Spitzbergen.

Remarks.—A histogram (Fig. 9) of the tube diameters in fragments of *Tabulipora urii* is bimodal. Two kinds of tubes are thus indicated to be present in this species and are inferred to occur in some others from qualitative examinations. In thin section, most of the tubes in the smaller *T. urii* group lack diaphragms and septa. Using the terminology of Dunaeva & Morozova (1967), these unpartitioned smaller tubes are referred to as exilapores; smaller tubes with partitions would be called mesopores if they were found in a species. The function of the exilapores is unknown. The most posterior portion of the tube in some specimens (Pl. 2, fig. 1d) has a diameter which falls into the exilapore class, but the anterior portion, which has a ring septum, fits into the larger-zooecia group. In this case, it would seem that an exilapore, or what would have been called an exilapore if the wider part of the tube had not been seen, eventually expanded to become a zooecium. Most of the exilapores, however, do not expand.

It is apparent that many synonyms exist among the 100 or so species which can be assigned to *Tabulipora*. Zoarial variability was not sufficiently understood when many of them were named and consequently too much weight was given to slight differences in the number, form, or position of various structures such as acanthopores and exilapores. Commonly, states of a character formerly used to distinguish species are found in a single zoarium. Much further research like that of Cuffey (1967) on zoarial variability needs to be done in order to build a workable basis for distinguishing species of this genus; until such work is accomplished, use of older quantitative data in species identification is bound to produce errors. Especially will this be so if one is dealing with many species described from the same area (e.g., *T. ramosa-T. cestriensis* complex) (Cuffey, 1967) and with species erected primarily on the basis of apparent quantitative dissimilarity with already named forms.

Previously unused but possible significant species characteristics have been found during this study. They include: 1) nature of ring septa, (i.e., size and shape of the foramina, and whether or not the rim around the foramen is thickened, proximally deflected, blunt, tapering to a thin edge, or otherwise uniquely shaped); 2) nature of exozone zooecial walls (i.e., their thickness, degree of annular thickening development, and cross-sectional size and shape of the annular thickenings); and 3) size of chambers formed between diaphragms (posterior walls) and ring septa (anterior walls).

Tabulipora might be divided into two genera in the manner used to distinguish *Stenopora* Lonsdale, 1844, and *Stenodiscus* Crockford, 1945, namely, presence or absence of diaphragms.

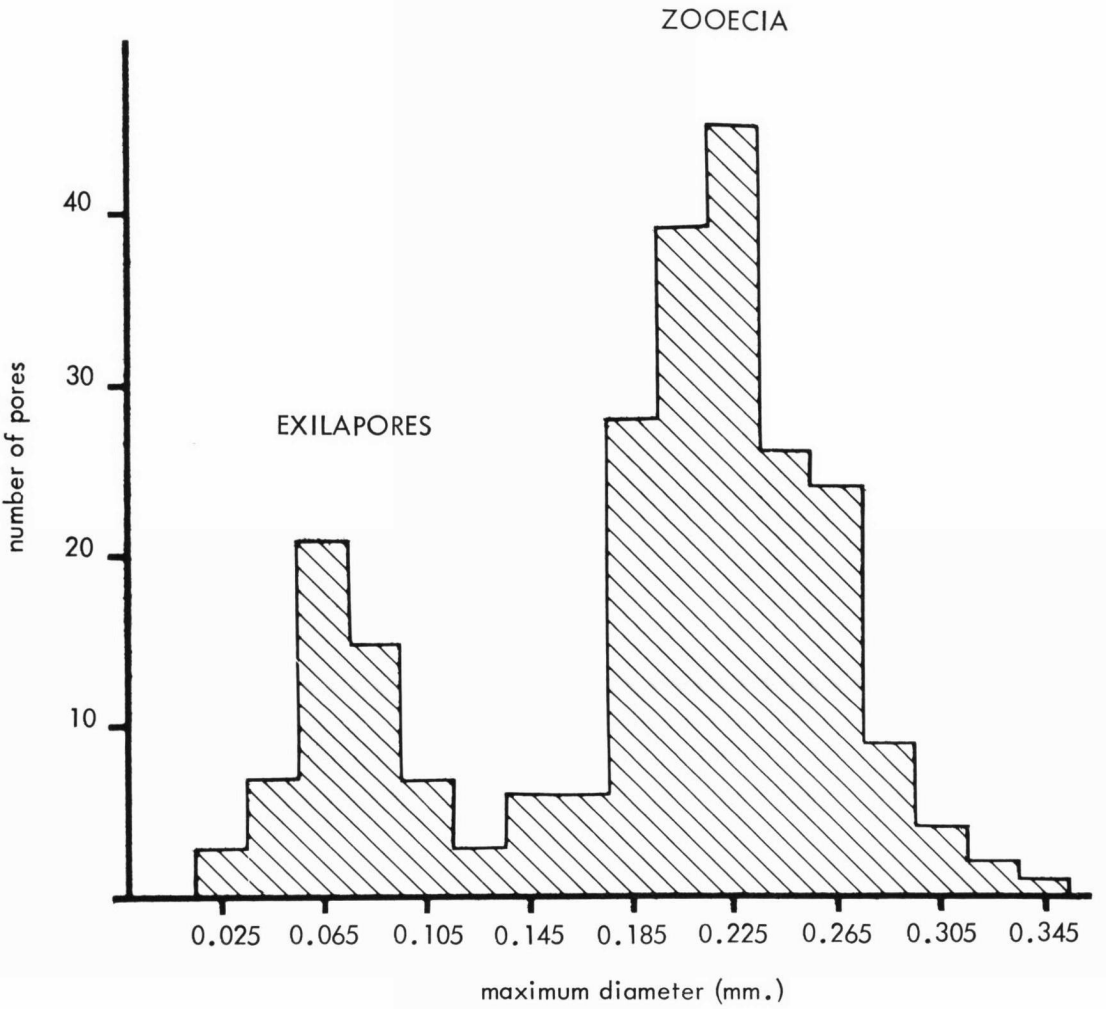
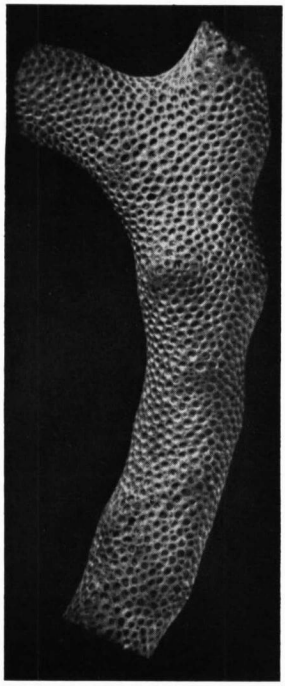


FIG. 9. Frequency diagram of tube diameters in *Tabulipora urii* (drawn from diameter measurement data for all tubes in 23 1-mm. squares in 10 different specimens).

EXPLANATION OF PLATE 7

FIGURE

1. *Tabulipora urii* (FLEMING, 1828), lectotype, Hunterian Mus. D.787, from Lower Limestone Series, upper Lower Carboniferous (Visean), East Kilbride, Scotland.——1a. External view of zoarium, ×5.——1b. External view showing distally offset ring septa, acanthopores, and mural tubuli in area of branch bifurcation, ×30.——1c. Tangential section showing distally offset ring septa, acanthopores indenting zooecial cavities, thick walls of annular thickenings and intervening thin walls, ×30.——1d. Transverse section showing irregularly arranged zooecia of endozone and interzooecial layers of annular thickenings in exozone, ×30.——1e. Longitudinal section showing zooecia bending abruptly at base of exozone, ring septa in outer endozone and exozone, and interzooecial layers of annular thickenings, ×30.



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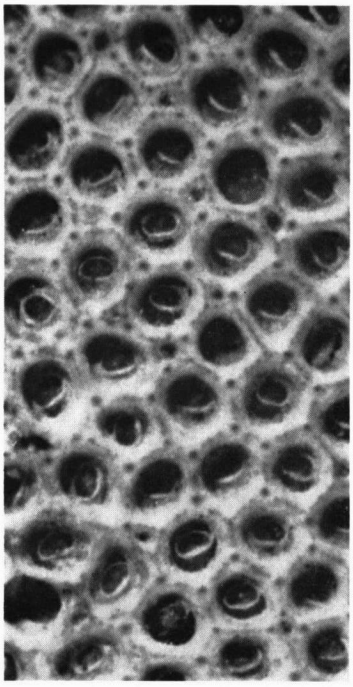

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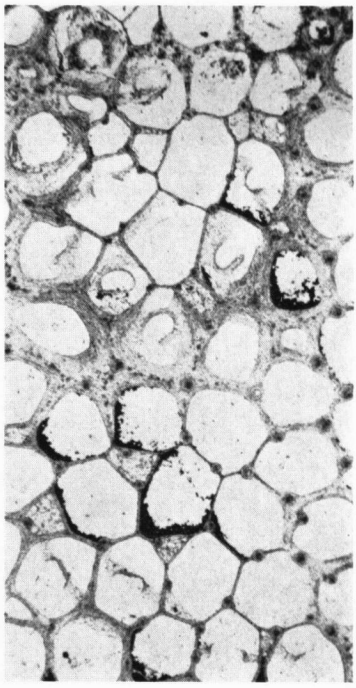

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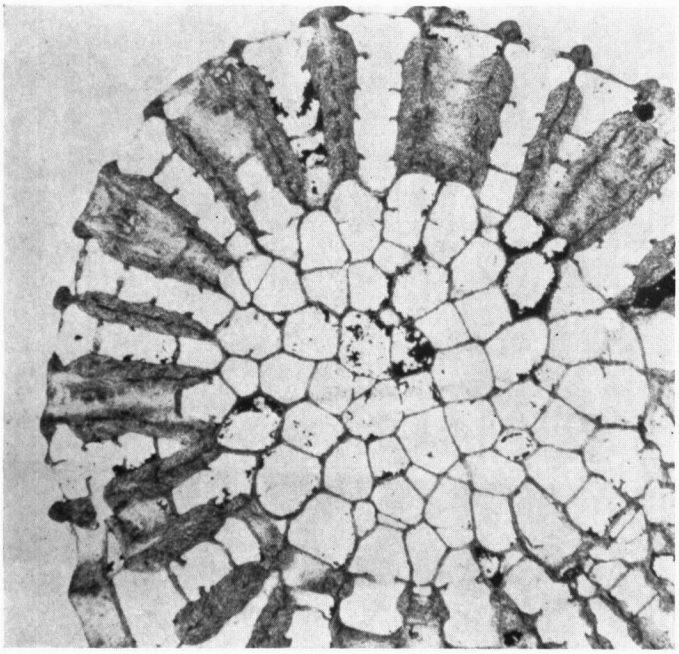

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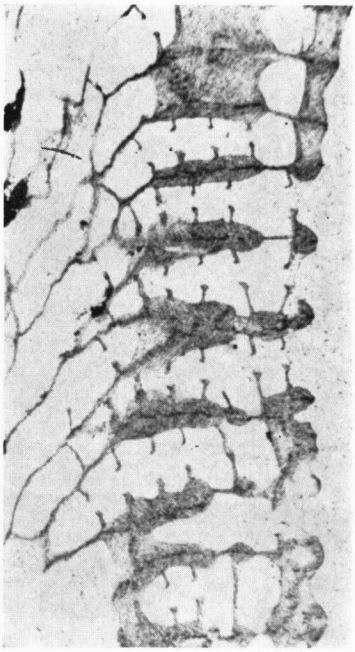

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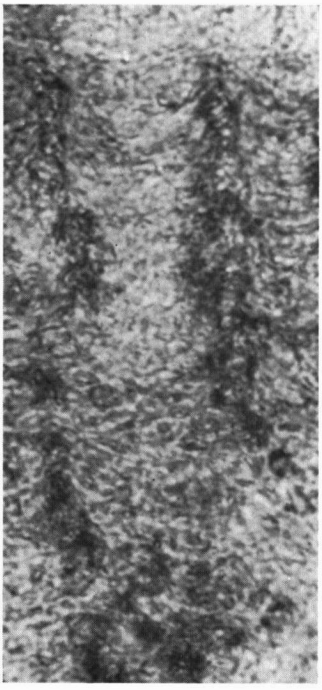

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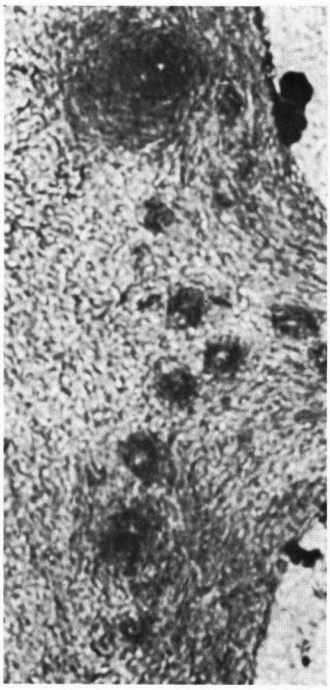

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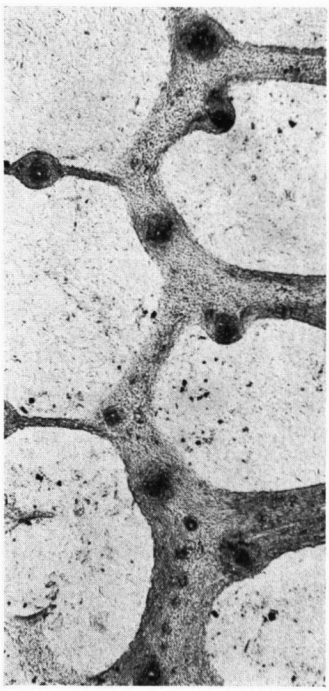

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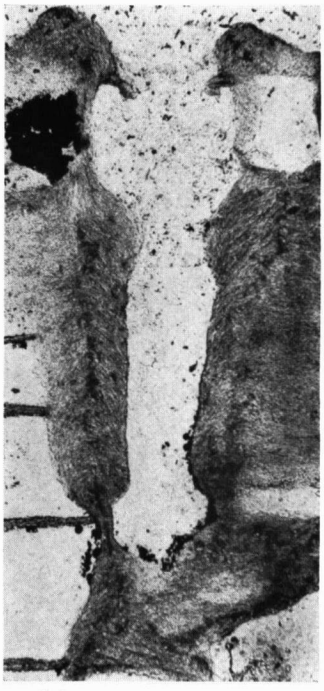

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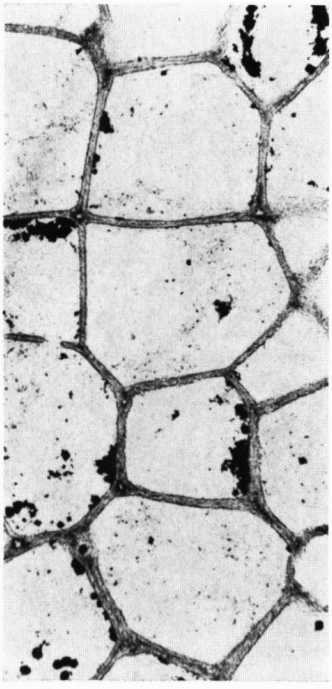

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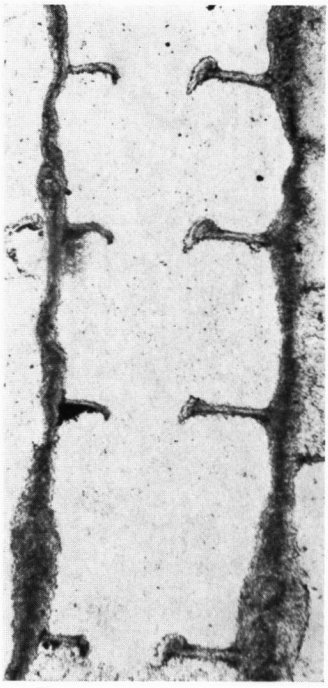

2

However, it was pointed out in a previous section that less calcified diaphragms which were not preserved may have existed in some species of *Tabulipora*. Furthermore, foraminal plates, though rare in some forms, are present in most.

For similar reasons, one might instead question the validity of separating *Stenodiscus* and *Stenopora*. The diaphragms of *Stenodiscus*, as seen in the type specimens of its type species (*S. moniliformis* CROCKFORD, 1945), have the same brown coloration as those in *Tabulipora*. If this coloration indicates a high organic content, the diaphragms of *Stenodiscus* may not always have been preserved. Further evidence should be sought to clarify the status of *Stenopora* and *Stenodiscus* in this regard.

Amphiporella GIRTY (1910) was considered different from *Tabulipora* because of its frondose growth habit and presence of exilapores. However, *Tabulipora* also has exilapores, and exhibits such a variety of growth habits that frondose species cannot be excluded, although none yet have been described. BASSLER (1941) and Ross & Ross (1962) have suggested that *Amphiporella* constitutes only a form of *Tabulipora*, and accordingly the two genera are considered synonymous here.

YANG (1950, p. 8) erected *Sinotabulipora*, stating that it differs from *Tabulipora* in having more exilapores, and from *Amphiporella* in not being bilaminar. However, the type species of *Amphiporella* (*A. maculosa* GIRTY, 1910) is not bilaminar (i.e., bifoliate) and YANG's photos of *S. chaoi* do not illustrate an abundance of exilapores greater than in some fragments of *Tabulipora* species. Therefore, *Tabulipora* and *Amphiporella* are here considered senior subjective synonyms of *Sinotabulipora*.

TABULIPORA URII (Fleming, 1828)

Figure 1; Plates 7-8

Cellepora urii FLEMING, 1828, p. 532.
Tabulipora urii YOUNG, 1883.
Tabulipora urei LEE, 1912.

MATERIAL.—*Hunterian Museum, Glasgow, Scotland:* Ure collection from Lower Limestone Group (Lower Carboniferous), East Kilbride, Scotland; lectotype, D.787 (3 sections, 5 acetate peels with 27 assorted duplicates, 1 remnant); paralectotypes, D.785, D.786, D.907/1-60, D.900 (1 section, no remnant), D.901 (1 section, no remnant), D.902 (1 section, 1 peel, no remnant), D.903 (1 peel, 10 transverse serial peels, 1 remnant), D.904 (9 transverse serial peels, 1 remnant), D.905 (9 transverse serial peels, 1 remnant), D.906 (9 tangential serial peels, 1 remnant). Young collection, Carboniferous, southern Scotland; D.300, D.301 (7 specimens, sections D.301a, b) (Capelrigg Quarry, East Kilbride), D.304-D.305 (1 section) (Hillhead Quarry, Beith), D.306 (1 section) (Boghead Quarry near Hamilton), D.307 (1 section) (Howood near Paisley).

National Museum of Natural History, Washington, D.C.: Collection from Lower Limestone Group (Lower Carboniferous), Hillhead Quarry, Beith, Ayrshire, Scotland (USNM loc. 14025) given by John Young; 14025-1 (2 sections), 14025-2 (2 sections), 14025-3 (3 sections), 14025-4 (1 old section); 11 uncut specimens.

DESCRIPTIONS.—Zoaria ramose or incrusting, branches generally less than 4 mm. in diameter.

Zooecia in endozone bend toward exozone at constantly increasing angle, bending more abruptly in base of exozone to become nearly or quite perpendicular to lateral surface. Endozone zooecial walls mainly thin. New zooecia bud anywhere within endozone but mostly in groups aligned along distally arched zones extending from base of exozone to axis of branch. Small acanthopores with distinct central tubes and few to no concentric laminae common in endozone

EXPLANATION OF PLATE 8

FIGURE

1. *Tabulipora urii* (FLEMING, 1828), lectotype, Hunterian Mus. D.787, from Lower Limestone Series, upper Lower Carboniferous (Viscan), East Kilbride, Scotland.——1a. Longitudinal section showing mural tubuli, ×400.——1b. Tangential section showing mural tubuli and acanthopore, ×400.——1c. Tangential section showing mural tubuli, acanthopores, structure of zooecial walls, ×100.——1d. Longitudinal section of small zooecium with terminal ring septum, ×100.——1e. Transverse section of part of zoarium showing endozone acanthopore canals lacking concentric laminae, ×100.
2. *Tabulipora urii* (FLEMING, 1828), paralectotype, Hunterian Mus. D.900, from Lower Limestone Series, upper Lower Carboniferous (Visean), East Kilbride, Scotland. Longitudinal section of zooecium showing ring septa with distal side of foramen rim posteriorly deflected, proximal side posteriorly deflected and thickened anteriorly, ×100.

zooecial corners. Diaphragms absent. Ring septa rare in inner endozone but a few occur in outer portions. Endozone zooecial walls thicken slightly near base of exozone.

Exozone zooecial walls greatly thickened in long segments or short annular thickenings separated by thin-walled zones; annular thickenings and thin-walled segments commonly arranged in interzooecial layers. Cross sections of annular thickenings generally oval. Thicker walls with U-shaped laminae, thinner walls with V-shaped laminae; discontinuous dark zone along zooecial boundary. Zooecial boundaries polygonal in tangential section; zooecial cavities vary from polygonal to rounded as walls range from thin to thick.

Diaphragms absent in exozone. Ring septa common throughout exozone, generally spaced less than a zooecial diameter apart; some inclined distally; many in interzooecial layers. Foramina kidney-shaped, most offset distally with straighter side proximal. Ring septa composed of V-shaped laminae pointing toward zooecial axes (posteriorly in deflected rims). In cross sections dark line can generally be seen connecting points of V-shaped laminae; this line near and parallel to posterior surface of septum. Anterior segments of V-shaped laminae nearest zooecial walls continuous with wall laminae at least part way around septum. Proximal sides of ring septa generally slightly thicker than distal sides. Rims around foramina deflected posteriorly and anterior surface of rim thickened on proximal side. Foraminal plates absent.

In exozone large well-defined acanthopores with central tubes are common in and between zooecial corners. Some do not pass along zooecial boundaries but are offset into zooecial cavities. Some connect with acanthopores in endozone. Where they cross thin-walled segments separating annular thickenings they retain their diameters, thus inflecting zooecial cavities.

Mural tubuli common in groups or rows in thicker walls, forming tubercles on surface. Mural lacunae common.

Exilapores common. Monticules formed by clusters of smaller zooecia.

Stratigraphic and Geographic Distribution. —Lower Limestone Group (Lower Carboniferous), southern Scotland.

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